National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

LYNX RECRUITMENT IN RELATION TO SNOWSHOE HARE DENSITY

BY

GARTH MOWAT

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of **Master of Science.**

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta

Fall 1993

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-88035-X

Canada

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: **Garth Mowat**

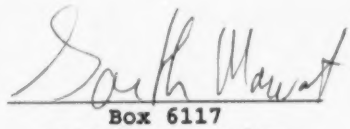
TITLE OF THESIS: **Lynx Recruitment in Relation to Snowshoe Hare Density**

DEGREE: **Master of Science**

YEAR THIS DEGREE GRANTED: **1993**

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.



Box 6117
Whitehorse, Yukon
Y1A 5L6

25 May 1993

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **LYNX RECRUITMENT IN RELATION TO SNOWSHOE HARE DENSITY** here submitted by **GARTH MOWAT** in partial fulfilment of the requirements for the degree of **MASTER OF SCIENCE.**

Dr. Stan Boutin

Dr. John Holmes

Dr. Mark Dale

Dr. Greg Henry

25 May 1993

ABSTRACT

Litter size, birth rate (proportion of females with young in mid-June), and survival of young to winter were estimated for lynx (*Felis lynx*) in southwest Yukon between 1990 and 1992. Radio-collared females were located shortly after parturition to count young, and then again in the winter to count, by their tracks in the snow, the number of young still alive. In utero litter size and pregnancy rate were estimated by counting placental scars on uteri taken from lynx carcasses collected from trappers working around the study area. Hare (*Lepus americanus*) density, as estimated by pellet transects, peaked in 1990 and began to decline in winter 1990-91. Reproducing lynx faced their first declining food supply in spring 1991.

Litter size averaged 5.3 (n = 12) for adults (>2 years) and 4.2 (n = 5) for yearlings in 1990, and all females monitored gave birth. Adult litter size was 4.9 in 1991 (n = 15) and 16 of 19 adult females (84%) had litters in mid-June. Zero of 7 yearlings retained litters to mid-June in 1991. In 1992 none of the 7 adult or 3 yearling females monitored gave birth. Minimum survival estimated from track counts was 0.63 in 1990 and 0.75 in 1991 for kittens of adult mothers. Survival was 0.26 in 1990 for kittens of yearlings. Recruitment to one year of age was 2.8 kittens per adult female, and 0.55 kittens per yearling female in 1990. In 1991 recruitment was 3.2 from adults and 0.08 from yearlings.

In utero estimates of litter size and pregnancy rate were closest to live reproductive rates when light placental scars were excluded. When light scars were excluded both litter size and pregnancy rate tended to be lower in utero, though only slightly for litter size. Methods for classifying placental scars to achieve the most accurate estimates of litter size and pregnancy rate are discussed.

Lynx recruitment went from a peak in 1990 to zero reproductive output in 1992. Adult females managed to recruit young the year after the hare peak, but recruitment from yearlings virtually ceased in the first year of the decline phase. Recruitment from yearlings was surprisingly low, even the year of the hare peak. If this observation describes the greater population it has serious ramifications for trapped populations, which are often comprised largely of yearlings. Population models which have based yearling recruitment on in utero estimates of reproduction are likely to have over-estimated recruitment.

ACKNOWLEDGEMENT

I thank all the technicians and volunteers who have worked on this study, especially: the Denisons, Rick Ward, Torrie Hunter, Ken Frankish, and René Rivard. Brian Slough and Stan Boutin have both been very patient with the logistics and the writing of this thesis. I have learned volumes from the discussion with staff and students in the Zoology department, and especially the "Stan Clan" on the 10th and 11th floors, in which I include Barb Thomas. Numerous people have reviewed proposals, outlines, and chapters of this thesis and to them I owe my thanks. The Yukon Territorial Government-Fish and Wildlife Branch, Canadian Wildlife Service-University Research Support Fund, Canadian Circumpolar Institute-BAR, and the Canadian Dept. of Indian and Northern Development-Northern studies training grant, all provided funding for this work. Finally, I would like to thank Marie-Odile Amiet for her patience, and her scrutinous review of my use of the English language.

TABLE OF CONTENTS

GENERAL INTRODUCTION 1
LITERATURE CITED 2

CHAPTER I
LYNX RECRUITMENT DURING A SNOWSHOE HARE POPULATION PEAK AND CRASH IN SOUTHWEST YUKON.

I.1. INTRODUCTION 3

I.2. STUDY AREA 3

I.3. STUDY BACKGROUND 4

I.4. METHODS
I.4.1. Hare Abundance 4
I.4.2. Lynx Reproduction 4
I.4.3. Kitten Survival 5

I.5. RESULTS
I.5.1. Hare Density 7
I.5.2. Birth Rate of Lynx 7
I.5.3. Litter Size and Date of Birth 7
I.5.4. Kitten Sex and Weight 8
I.5.5. Family Group Fidelity in Winter 8
I.5.6. The Validity of Snow Tracking 9
I.5.7. Winter Litter Size 9
I.5.8. Kittens per Female in Winter 9
I.5.9. Kitten Survival from Birth to Late Winter 9
I.5.10. Kitten Survival from Late Winter to June 10

I.6. DISCUSSION
I.6.1. Hare Density 10
I.6.2. Pregnancy Rate 11
I.6.3. Litter Size 11
I.6.4. Winter Litter Size 12
I.6.5. Kitten Survival 12
I.6.6. Snow Tracking 13
I.6.7. Litter Size, Date of Birth, and Kitten Sexing 13

I.7. MANAGEMENT IMPLICATIONS 14

I.8. LITERATURE CITED 23

CHAPTER II
USING PLACENTAL SCAR COUNTS TO ESTIMATE LITTER SIZE AND PREGNANCY RATE IN LYNX.

II.1. INTRODUCTION 25

II.2. METHODS 26

II.3. RESULTS
- II.3.1. Does Refreezing of Uteri Affect Scar Shade? 27
- II.3.2. Variation in Scar Shade Within a Litter 27
- II.3.3. Intra-uterine Mortality of Young 28
- II.3.4. Do Scars Fade Over the Trapping Season? 28
- II.3.5. Reproduction Differences Among Habitats 28
- II.3.6. In Utero vs Post-Partum Estimates of Litter Size . . . 28
- II.3.7. Pregnancy Rates vs Birth Rates 29
- II.3.8. Effects of Ageing Lynx on Litter Size 29

II.4. DISCUSSION
- II.4.1. Handling of Uteri 29
- II.4.2. Variation in Scar Shades Within Litters 30
- II.4.3. Intra-uterine Mortality of Young 30
- II.4.4. Fading of Scars Over the Trapping Season 31
- II.4.5. What Scars to Use to Estimate Litter Size and Pregnancy rate 31

II.5. SUMMARY AND RECOMMENDATIONS 33

II.6. LITERATURE CITED 44

GENERAL DISCUSSION AND CONCLUSIONS 47
LITERATURE CITED 49

LIST OF TABLES

Table		Page
I-1	Reproductive statistics from lynx litters of radio-collared resident females located in mid-June during a hare peak (1990-91) and crash year (1991-92) in SW Yukon.	15
I-2	The number of locations of radio-collared kitten lynx that were on and off their mother's home range, in SW Yukon winter 1990-91 and 1991-92.	16
I-3	Average mid-winter litter size for lynx in SW Yukon during a peak and crash year in hare numbers.	17
I-4	Average number of kittens per female, in mid-winter, on the Snafu lake study area in SW Yukon during a hare peak and crash year.	18
I-5	Minimum survival of kittens and litters on the Snafu lake study area in SW Yukon during hare peak and decline years.	19
I-6	Pregnancy rate and litter size for selected North American lynx populations at the cyclic peak.	20
I-7	Summary of estimates of reproduction and recruitment for lynx during a hare peak and crash year in SW Yukon.	21
II-1	Placental scar counts and live litter size for radio-collared female lynx from SW Yukon.	35

LIST OF FIGURES

Figure — Page

I-1 Snowshoe hare density (hares/ha) for our 282 km² study area in SW Yukon. 22

II-1 The proportion of yearling and adult lynx with light and dark placental scars. 36

II-2 The proportion of placental scars that were scored light on adult and yearling lynx uteri from SW Yukon. 37

II-3 The number of carcasses collected per month from fur trappers in SW Yukon between 1989-90 and 1991-92. 38

II-4 The proportion of females with light and dark placental scars during 3 periods of harvest (Nov-Dec, Jan, Feb-Mar) for lynx carcasses from SW Yukon, 1989-90 to 1991-92. 39

II-5 Litter sizes of adult lynx during 1989 to 1991 resulting from the combination of placental scars of different shades. 40

II-6 Litter sizes of yearling lynx during 1989 to 1991 resulting from the combination of placental scars of different shades. 41

II-7 Pregnancy rates of adult lynx during 1989 to 1991 resulting from the combination of placental scars of different shades. 42

II-8 Pregnancy rates of yearling lynx during 1989 to 1991 resulting from the combination of placental scars of different shades. 43

GENERAL INTRODUCTION

The lynx (*Felis lynx*) is widely distributed throughout boreal North America and was the second most economically important species to northern trappers through the 1980's (Stats. Canada 1991). Lynx populations follow the ten year cycle of the snowshoe hare (*Lepus americanus*) and are reported to lag behind by one year (Keith 1963). Trapping is believed to have caused major declines in several North American lynx populations (Todd 1985, Bailey et al. 1986), and recent studies using radio-telemetry have shown extremely high mortality due to trapping (Parker et al. 1983, Ward and Krebs 1985, Bailey et al. 1986). Brand and Keith (1979) suggested that more pro-active management of lynx harvest during the low period of the hare cycle (3-4 years) was necessary to reduce the chance of widespread population declines (see Todd 1985). In 1986, high market prices and the threat of over-harvest compelled the Yukon Wildlife Branch to begin a study of the impact of harvest on Yukon lynx (see Slough and Ward 1990).

Previous work in Alberta attempted to assess the impact of trapping (Brand and Keith 1979) by modelling the Alberta lynx population. Their model predicted that curtailing harvest during years of low recruitment would increase the entire ten year harvest and the long-term stability of the lynx population. Lynx are managed in Yukon by a refugia-based system, where untrapped areas provide recruitment into trapped areas throughout the hare cycle. Furbearer managers in Yukon obtained similar results to Brand and Keith (1979) when they modelled the Yukon lynx population (Mowat and Slough unpubl. data). However, different values for juvenile recruitment and adult survival markedly affected the resilience of the population to harvest during the hare low and the total 10 year harvest. The usefulness of suspending harvest during hare lows depended on recruitment and survival rates. This study was designed to provide accurate reproductive data to northern furbearer managers to investigate the impact of harvest on lynx populations, and to enable them to conclude whether the tracking or refuge strategies are superior in their respective regions. Results will be combined with estimates of survival and density from the Yukon lynx program for this investigation. The impact of various harvest regimes on a model lynx population will be used to assess current lynx management.

Placental scar counts are commonly used to estimate or index reproductive parameters in small and medium size mammals (Gilbert 1987). However few studies have assessed how well placental scar counts reflect live pregnancy rate and litter size (Macphersen 1969, Englund 1970, Crowe 1975, Brand and Keith 1979, Lindstrom 1981). This is the first study to compare in utero estimates of litter size and pregnancy rate with rates from a free living population. This comparison will test the accuracy of placental scar counts for estimating actual reproduction in lynx.

LITERATURE CITED

Bailey, T. N., E. E. Bangs, M. R. Portner, J. C. Malloy, and R. J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. J. Wildl. Manage. 50:279-289.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827-849.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. J. Mamm. 56(3):177-198.

Englund, J. 1970. Some aspects of reproduction and mortality in Swedish foxes (*Vulpes vulpes*) 1961-63 and 1966-69. Swedish Wildlife. 8:1-82.

Gilbert, F. F. 1987. Methods for assessing reproductive characteristics of furbearers. Pages 180-190 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Keith, L. B. 1963. Wildlife's ten year cycle. Univ. of Wisconsin Press, Madison. 201pp.

Lindstrom, E. 1981. Reliability of placental scar counts in red fox (*Vulpes vulpes*) with special reference to the fading of the scars. Mamm. Rev. 11(4):137-149.

Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. Can. Wildl. Ser., Rep. Ser. 8. 52pp.

Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx on Cape Breton Island. Can. J. Zool. 61:770-786.

Slough, B. G., and R. M. P. Ward. 1990. Lynx harvest study 1988/1989. Yukon Fish & Wildl. Branch, unpubl. Progress Report. 74pp.

Statistics Canada. 1991. Fur Production 1989-90. Ministry of Supply and Services Canada, Ottawa.

Todd, A. W. 1985. The Canada lynx:ecology and management. Can. Trapper. 13(2):15-20.

Ward, R. M. P., and C. J. Krebs. 1985. Behavioral responses of lynx to declining snowshoe hare abundance. Can. J. Zool. 63:2817-2824

CHAPTER I. LYNX RECRUITMENT DURING A SNOWSHOE HARE POPULATION PEAK AND DECLINE IN SOUTHWEST YUKON

I.1. INTRODUCTION

Modelling of the Alberta lynx (*Felis lynx*) population by Brand and Keith (1979) suggested that populations were less resilient when harvested through the cyclic hare low. Their results show that restricting harvest during cyclic lows would result in an increased 10 year harvest and less risk of over-harvest to the lynx population. Caughley (1977:197) suggested that the only way to manage a cyclic population, with a periodicity greater than about 5 years, is to restrict harvest when the population growth rate is negative and allow harvest when it is positive; a plan he called a 'tracking strategy'. Refugia management is an alternative to this strategy. This method leaves certain areas untrapped throughout the hare cycle so they can provide recruitment into trapped areas, especially during the hare increase phase. Managers need to know which strategy is less likely to result in population declines, and which strategy will provide the greatest ten year harvest for lynx. Complete closure of lynx harvest for several years would be a difficult program to implement, especially in areas where harvest cannot be shown to be excessive and large untrapped areas exist, such as in northern Canada. It is likely to be feasible only where it can be shown to benefit both trappers and lynx populations.

Brand and Keith (1979) concluded that recruitment was the most important parameter causing the decline in lynx numbers that follows the hare crash. Their model is the only attempt at estimating lynx recruitment to the yearling cohort. To do this they had to make several assumptions: 1) They extrapolated spring and late-winter lynx densities from their Rochester study area to all suitable lynx habitat in Alberta. 2) They assumed lynx survival from the first to the second winter of life was the same as that of adult lynx. 3) They assumed that yearlings were trapped in proportion to their abundance. 4) They further assumed laboratory derived estimates of pregnancy rate and litter size were accurate. The impact of harvest on lynx populations could be more conclusively assessed if estimates of recruitment were available that are not contingent on the above assumptions.

Many studies have estimated pregnancy rate and litter size in lynx by counting placental scars on uteri or corpora lutea in ovaries taken from trapped lynx (Nava 1970, O'Connor 1984, Parker et al. 1983, Quinn and Thompson 1987). From the above studies reproduction is known to decrease with declining hare density. Only one field study has estimated juvenile lynx survival and it documented marked changes in winter litter size with hare density (Brand et al. 1976). However sample sizes were small (2-4 litters) and litter size at birth was unknown. Pregnancy rates and age-specific recruitment have not yet been assessed in the field. The relative importance of changes in pregnancy, litter size and juvenile survival to lynx recruitment remains unclear.

The objectives of this study were to estimate juvenile recruitment of lynx and to document the relationship between recruitment and hare density. Estimates of pregnancy, litter size, and survival were obtained from a free living population in an effort to describe these parameters and to assess their importance to population growth. These data, combined with accurate estimates of survival and density, will provide a more thorough investigation of the impacts of harvest through the hare cycle than was possible for Brand and Keith (1979), and lead to an assessment of the practical benefit of the tracking and refugia strategies for all harvested lynx populations.

I.2. STUDY AREA

The study site was at Snafu Lake (133° W, 60° N) which is 110

kilometres southeast of Whitehorse, Yukon. The area was 282 km² and ranged in elevation from 900 to 1500 meters. It was characterized by rolling hills and wide valleys with numerous small lakes. Most of the area was burned in 1958. Regenerating lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) stands were interspersed with small unburned stands of mature pine and spruce, and sub-alpine fir (*Abies lasiocarpa*) at higher elevations. About 90% of the area was boreal forest. The remaining 10% was open water, meadows dominated by sedge (*Carex spp.*) and willow (*Salix spp.*), and continuous patches of alpine tundra at higher elevations. The study site was half of a registered trapping concession which had not been trapped for about ten years. The surrounding concessions were trapped by fur trappers intermittently. The study area was part of a continuous area of approximately 500 km² that was untrapped during this study.

I.3. STUDY BACKGROUND

This area has been the site of an intensive lynx population study since 1986 (Slough and Ward 1990). Each winter from 1986-87 to 1991-92 most lynx on the study area were live-trapped and radio-collared. All adult females captured were radio-collared. Kittens were aged by body weight and adults by cementum analysis of incisor teeth removed at capture (Brand and Keith 1979, Quinn and Parker 1987:689). Only 2 of the yearlings followed during this study required ageing by cementum analysis. Sixteen others had been captured previously as kittens. Weekly aerial locations were done throughout the year to document the movements, home ranges, and fates of radio-collared animals.

I.4. METHODS

I.4.1. Hare Abundance

Hare abundance was estimated by counting fecal pellets in 480 individual quadrats each June of 1990-1992. These quadrats were 5.1 cm X 305 cm in size and were placed along transects at 9.14 m intervals (as in Krebs et al. 1987). Each of the 11 transects contained 20-50 quadrats and every quadrat was subjectively classified into 1 of 7 habitat types. Transects began along the shore of accessible lakes, and an attempt was made to sample all the major habitat types on the study area. It is unknown if the individual quadrats sampled habitat types in proportion to their occurrence on the study site.

I used a more recent equation to calculate hare density than that in Krebs et al. (1987) based on a log transformation of both variables and using GMR regression (C. J. Krebs, Univ. of B. C., pers. commun.: Ricker 1973)

I.4.2. Lynx Reproduction

Resident radio-collared female lynx were located from the air 4 to 10 times between May 20 and June 20, 1990-1992. Parturition was inferred when the female was repeatedly located in the same place; I then tracked the female to the nest site on the ground. Each kitten was ear-tagged, weighed and sexed. Ear-tags (size 2, style 1005 monel tags, National Band and Tag Co., Newport, KY) were inserted around or through a vertical cartilage low in the ear. About half the tag was left hanging out of the ear so there was space for the ear to grow without the tag tearing the ear. Sex was determined by the relative distance between the urinogenital opening and the anus. Male openings were about twice as far apart as female openings and in older kittens, males had hair between the openings. Six litters had been handled in this manner before 1990. At least four of these had survivors to the winter suggesting tagging did not cause abandonment by female lynx. During

this study, about half the females moved back to the litter before we left the site. Females cleaned the kittens immediately but we saw no sign of infanticide. Aerial locations done after tagging indicated females often moved their young several hundred meters after tagging but did not abandon their litters.

Females that continued to move during the parturition period were considered not to have reproduced. These females may not have been pregnant, lost a litter before term, or lost their litter early in the lactation period. Normally I could not separate these three possibilities, but 3 females restricted their movements early in the parturition period but soon after began to make wide ranging movements. I assumed these females lost their litter at or shortly after parturition and considered them not to have given birth to live young. Other females may have done the same. Twenty females no longer had a litter in mid-June during this study and none of these were found to have a litter in the winter. I defined birth rate as the proportion of females with a litter in mid-June, when I located the nest sites. This rate is lower than the pregnancy rate because some litters were lost between birth and tagging.

Jackson (1987) has calculated regressions of age on weight for both sexes of bobcats (*Felis rufus*), and I used these to calculate the mean birth date for the adult and yearling cohorts. Regressions for either sex indicated the same date of birth. These dates are approximate because lynx kittens may have different birth weights (McCord and Cardoza 1982:737, Jackson 1987:15) or grow at different rates than bobcats. Also body weight may not predict age very precisely. Birth weight of domestic cats (*Felis silvestris*) is related to litter size, and growth rates vary with litter size (Deag et al. 1988:31-33) and presumably body condition of the female.

I.4.3. Kitten Survival

Lynx kittens stay with their mothers until late winter (Saunders 1963, Brand et al. 1976, Parker et al. 1983). Winter litter size was estimated by locating radio-collared females with hand-held telemetry gear and counting the size of the family group by their tracks in the snow. It was often necessary to follow a group of tracks for hundreds of metres before a count was possible. Occasionally I could not make a count, particularly when the group was hunting. Open areas with wind packed snow were best for doing counts because kittens often spread out to play.

Snow conditions, the age, and the location of each group of tracks affected the reliability of any single count. Kittens often followed in another lynx's tracks making complete enumeration difficult. Counting larger litters was more difficult than counting smaller ones because individuals in the group were more difficult to separate. For the above reasons, and the possibility a kitten was not with the female at the time of a count, each count was viewed as a minimum estimate. Two upward biases to track counts were possible. Kittens sometimes doubled back onto a previous set of tracks. I followed tracks for several hundred meters and feel I would have noticed this behaviour most of the time. Related female lynx were located together regularly when I was snow tracking and I tracked groups of up to 13 lynx. Reports of 8 or more lynx in a group are probably groups of two or more females with kittens (Hardy 1907 cited in McCord and Cardoza 1982:739). When both females had kittens, or both females were radio-collared classifying the groups as one family group was unlikely. If two females were together and only one had a litter then there was a possibility that the lone female (normally a yearling) would be included in the count. Yearling female tracks are difficult to tell from kittens and I regularly located solitary yearlings near, but less often with, their mothers' family group.

In 1990-91 snow tracking was done between mid-December and mid-

January and eleven litters were successfully counted. Five more litters were counted in March of that winter. In 1991-92 seven females were snow tracked in late December.

During live-trapping (Dec-Apr 15) I and other project technicians travelled trapping trails every day. We attempted to count the tracks of all family groups crossing our trapping trails. If the identity of the female lynx could not be determined with telemetry equipment, subsequent captures and home range estimates often allowed us to determine the female's identity based on the location of the home range or capture site. I classified female identity of these counts as being: 1) confirmed, 2) unconfirmed, 3) unknown. One confirmed or two similar unconfirmed counts, before early March, were accepted as a litter size estimate. When more than one confirmed count existed the larger was used for the estimate. If more than two unconfirmed counts existed the largest count with 2 observations was used.

In 1990-91, 128 counts were done on trapping trails and winter litter size was estimated for 20 of 26 residents. Forty of these counts were classified as confirmed or unconfirmed, and counts were repeated up to 5 times for some females. In 1991-92, 138 counts were done on trapping trails and winter litter size was estimated for 20 of 24 residents. Seventy counts were classified as female confirmed or not confirmed and the largest number of these counts for any one female was 7. Two thirds of the above counts occurred from December to February and the remainder took place in March and early April.

During winter live trapping, kitten captures were used to verify winter litter size counts. Captures of females often confirmed the presence or absence of kits, or the litter size. Some lynx marked as kittens were caught by fur trappers each year and these returns were also used to confirm litter size estimates. In each winter some females were captured for the first time and I classified each of these as *immigrants* or *new residents* based on their age, home range, and tracking from previous years. I will refer to females that were on the study area from June until the following winter as *resident* females. All the latter females were located in June to determine if they gave birth, and if they had, the litter was located. The final estimate of a female's winter litter size came from a combination of snow tracking, counts on trails, and capture information. The larger of the two former counts was normally used to estimate litter size because the number of kittens captured only exceeded these estimates once.

Thirty-six kittens that were tagged at birth were recaptured in winter and one 200 g kitten was incorrectly sexed. There was little chance of not identifying a kitten tagged at birth during winter trapping because all kittens were tagged in both ears, and the probability of a kitten losing both tags was only 0.002.

Winter litter size would be biased low if some kittens or litters were independent before March. Radio relocations of collared kittens were used to assess the independence of kittens through the winter. Kitten locations were compared to the 100% convex polygon home range ($n > 40$) of their mother (B. G. Slough, Yukon Fish and Wildl., unpubl. data). Locations were considered off the home range if they were >500 m (half the approximate location error) from the border of the home range.

Only about half of the litters tagged in spring could be tracked in winter due to death, dispersal, radio failure, or inaccessibility of the female. However litter counts were also done for some new females each winter. Mean mid-winter litter size, and kittens per female was calculated for both resident and new resident females. Finally the two estimates were combined to increase the sample size of the estimates.

Kitten survival to late-winter was calculated by comparing the number of kittens tagged in June with the number alive in winter. A second estimate of survival was derived by comparing the mean June and winter litter sizes.

I.5. RESULTS

I.5.1. Hare Density

The number of hare pellets per quadrat changed significantly between years of this study (F = 22.87; 2, 1418 df; P < 0.0001). Differences between habitat types were also significant (F = 35.36; 6, 1418 df; P < 0.0001) but the interaction between years and habitat types were not (F = 1.16; 12, 1418 df; P = 0.31). Because I was interested in the overall change in hare numbers on the study area, and all habitats followed the same pattern of change, I combined counts for each year and calculated mean hare density. Mean density was 5.7 hares/ha during 1989/90, increased to 7.4 in 1990/91, then declined to 4.7 in 1991/92 (Figure I-1). The more recent regression developed by C. J. Krebs (University of B. C., pers. commun.) is based on hare densities between 0.02-4.0 hares/ha. All three densities on my study area were greater than 4 hares/ha hence these estimates are only valid if the relationship is linear beyond 4 hares/ha.

My observations of hares and hare tracks support these patterns. However I saw a dramatic increase in hare sign from winter 1989/90 to early winter 1990 and an equally dramatic decline over the winter of 1990/91. Hare densities appeared to continue to decline through 1992-93. I believe actual changes in hare numbers were much greater than those shown by pellet data and that the decline in numbers began about December 1990.

I.5.2. Birth Rate of Lynx

The live birth rate declined dramatically for yearlings and adults from 100% during the hare peak (1990) to 0% 2 years after the peak. All adult females on the study area had litters (n = 13) in mid-June 1990, and 16 adult females (n = 19) had litters in 1991 resulting in a birth rate of 0.84. No litters were located for any of the 7 adult females on the study area in 1992. Five yearling females had litters in 1990 (n = 5) but in 1991, the first spring after the hare peak, no yearlings had litters in mid-June (n = 7). Only 3 yearlings were left on the study area by spring 1992 and none of these had litters.

I was unable to locate the litter of one radio-collared adult female in 1990 because she was continuously moving during the parturition period. Subsequent radio locations revealed that she had a litter in early July. One kitten was captured from this litter in March 1991 and it was roughly 25% smaller than average. In 1991 I was unable to locate the litters of 11 of 26 female lynx. One adult female had kittens but they were located too late, and were too large to catch by hand. The remaining 10 females (3 adults and 7 yearlings) did not appear to have kittens in mid-June. Movements based on radio locations indicated that 3 yearlings probably had litters in early June but lost or abandoned them soon after birth. Three adult females and 2 yearlings may have had litters, while 2 yearlings did not appear to give birth. Radio locations in July and early August confirmed that none of these females had a late litter. Snow tracking of 2 adult and 4 yearlings, that did not have litters, indicated none had young the following winter. Seven untagged kittens were live-trapped in winter 1991-92 and none appeared to belong to any of the females which I classed as not giving birth. None of the 10 females located in 1992 appeared to give birth, and no kitten tracks were seen on the study area during the winter of 1992-93.

I.5.3. Litter Size and Date of Birth

Litter size for adult females was 5.3 in 1990 and 4.9 in 1991; these were not significantly different (t = 0.61, 25 df, P = 0.55: see Table 1). Yearling litter size was 4.2 in 1990 and no yearling females

had kittens in 1991. In 1990 yearling litter size was not significantly smaller than the adult litter size (t = 1.37, 15 df, P = 0.19). Two observations indicate yearlings gave birth later than adults. Yearlings did not restrict their movements as early as those of adults, and kittens born to yearlings averaged 242 g at capture and were much smaller than those born to adults which averaged 640 g (t = 23.75, 82 df, P < 0.0001; Table 1). This difference was not due to kittens of yearlings being located later than adults; the median date of capture was similar for all litters (Kruskal-Wallis H = 2.37, 2 df, P = 0.31; Table 1). The mean date of birth for adult females was 28 May in both years. As mentioned in Section I.5.2, one adult female gave birth in early July 1990 which would make it four or five weeks later than the calculated norm. Four yearlings gave birth 2 weeks later than adults and a fifth gave birth at the end of June.

The litter of one yearling was located within a day of birth. It contained one stillborn kitten that was still wet and covered by placenta; the other kittens had been cleaned. Three females including the dead one weighed 175 g, while 2 males weighed 200 g each. Radio locations for this female were within 100 m of the nestsite 2 or 3 days before she gave birth. She may have been searching for or preparing the nestsite before parturition. Litter size ranged from 1-7 for adults and 3-5 for yearlings.

I.5.4. Kitten Sex and Weight

Mean weight of kittens from adults in 1990 (640) was lower than the mean (699) for adults in 1991 (t = -2.61, 135 df, P = 0.01) though they were tagged at the same time (Table I-1 and Section I.5.3). Male kittens born to adult females tended to be larger than their female siblings in 1990 (paired t = 1.76, n = 10 litters with both sexes, P = 0.11). There was no difference in male and female kitten weights for those born to adults in 1991 (paired t = 0.84, n=13 litters, P = 0.42: see Table 1). Sex ratio of kittens did not change among cohorts (χ^2 = 1.23, n = 157, 2 df, P = 0.54) though there was a trend to more males in 1991 (Table 1).

I.5.5. Family Group Fidelity in Winter

I compared kitten locations to their mother's home range to assess whether all kittens remain with the family group in winter. Lynx kittens were more likely to be located off their mother's home range in April and early May than between December and March (χ^2 = 15.04, n = 111, 2 df, P = 0.001). Three of 38 locations were 1 to 1.5 km off the female's home range between December and February, and 6 of 29 were 1 to 3 km off in March. Twenty-three of 49 locations varied from 1.5 to 20 km away in April-May.

Though kittens were generally on their mothers home range until at least March, it does not mean family groups were always together. I located kittens irregularly using ground telemetry and kittens were usually located with the mother until March. When I located a kitten that was separate from its mother I always found them together on the next occasion. Family groups were seen together until mid-April of both years. Solitary kitten tracks were rarely seen before March and some of those tracks may have been yearling females. Solitary kitten tracks became more common in March and in late March and April I saw groups of kitten tracks together without the female. I believe kittens made short ventures on their own throughout the winter but soon returned to the group. Kittens began to move independently in March though snow tracking indicated many were not truly independent until late in April. I infer that snow tracking could be used to reliably estimate group size until late March though counts done before March 1 may have been more accurate.

I.5.6. The Validity of Snow Tracking

Late-winter litter size was estimated for 21 females in 1990-91 and 6 were found to have no kittens. A marked kitten was subsequently captured whose mother was a yearling female for which the track count was zero. Kittens were captured from 12 of 15 females believed to have kittens and for 7 of these females the snow tracking estimate was equal to the number of kittens live-captured. In 1991-92 kittens were captured for 8 of 14 non-zero counts but in only one case did the capture number equal the snow tracking estimate. There were 4 counts of zero in 1991-92 and no kittens that belonged to these females were captured. No kitten tracks were seen nor were any kittens captured during the winter of 1992-93.

I.5.7. Winter Litter Size

During the winter of 1990-91 five new adult females were captured and their litters counted. Three new adult females were assumed to be residents because they were captured in border areas of the study area that had not been livetrapped before. Two new adult females were termed immigrants and excluded from winter litter size estimates because they occupied home ranges that had been intensively trapped the year before. They were caught immediately after traps were set indicating no previous experience with traps. Neither of these two immigrant females had kittens and a third probable immigrant was not tracked but did not appear to have kittens either. Three new yearling females were captured in 1990-91 and one had been tagged as a kitten in June 1989. I assume all new yearlings were residents because none of the 5 radio-collared female kittens emigrated that year.

In 1991-92 one new resident adult female was captured on the border of the study area and her litter was counted. One new resident yearling was captured and she had a litter of two. Four females with kittens were tracked but not captured. These females were classified as new resident females because kitten captures, subsequent home range estimates, and tracking from previous years, suggested these females had litters the previous year and were therefore resident adults.

Mid-winter litter size of adult females was 3.3 in 1990-91 and 3.7 in 1991-92 (Table I-3). Differences between estimates for resident and new females were small for adults. Yearling litter size was 1.4 in 1990-91 and 0.4 in 1991-92 (Table I-3). The 1990-91 estimates for resident and new yearling females are different because 2 of 3 new yearlings had litters of 3, while only 1 kitten survived from 3 litters of residents.

I.5.8. Kittens per Female in Winter

The mean number of kittens per adult female on the study area in winter was 2.9 in 1990-91 and 3.2 in 1991-92 (Table I-4). These estimates differ from mean late-winter litter size because females that did not have kittens were included in this calculation. Estimates for resident females included counts for females that did not have litters in mid-June. Estimates for new females included counts of suspected immigrant females that had no kittens, and in 1991-92, counts of females that were never captured but were believed to be resident adults.

I.5.9. Kitten Survival From Birth to Late Winter

Survival of lynx kittens born to adults was 0.66 ($\underline{n}$ = 38) in 1990-91 and 0.83 ($\underline{n}$ = 36) in 1991-92 (Table I-5). Survival of kittens born to yearlings in 1990-91 was 0.08 though the sample size was small ($\underline{n}$ =

12). Low survival of kittens from yearlings was mostly due to loss of entire litters (2 of 3 lost). In 1991 the loss of yearling litters before term or shortly after made estimation of kitten survival impossible. Adults that had a litter in mid-June never lost the entire litter before mid-winter.

A second estimate of kitten survival was calculated by dividing mean winter litter size by mean spring litter size. The estimates for adults were 0.61 ($\underline{n}$ = 12/12 winter/spring) in 1990-91 and 0.75 ($\underline{n}$ = 13/15) in 1991-92 and are similar to the previous estimates of kitten survival. Note that sample size is the number of litters counted because the experimental unit is the litter here. Survival was 0.26 ($\underline{n}$ = 6/5) for kittens of yearlings in 1990-91 which is considerably larger than the previous estimate of kitten survival. This is probably a more realistic estimate because it includes data from 6 litters while the kitten survival estimate includes data from only 3.

Four resident and one new female died during this study. None of these were snow tracked well enough to include the fates of their kittens in the estimates of kitten survival. Therefore my estimates of kitten survival do not take into account the reduced chance of survival for kittens who's mother died while they are still dependent on her. This may be an important source of kitten mortality in trapped areas. Two females that died before Christmas appeared not to have any kittens survive, but three females that died after February 1 all left kittens that survived until April. The timing of the female's death probably affects the chance of survival of the kittens.

I.5.10. Kitten Survival From Late Winter to June

Thirteen kittens were radio-collared between 7 December 1990 and 29 March 1991. Four males emigrated in May and the remainder of these animals (9) stayed on the study area to yearling age. Nine kittens were captured between 19 February and 14 April 1992 and 1 male and 3 females left the area in April, and 2 males left in May. The remaining three animals stayed on the study area into their yearling year. None of the litters that were snow tracked repeatedly in 1990-91 and 1991-92 appeared to lose any members over the winter. Though sample sizes were small, it is clear that survival of kittens from winter until they become yearlings is high. The risk of mortality may increase for those animals that emigrate but this risk was minimal to the kitten cohort because most animals did not leave until just before their first birthday.

I.6. DISCUSSION

I.6.1. Hare Density

Hare numbers increased until the winter of 1990-91. Exactly when hares began to decline is unknown but they were certainly less abundant by the lynx breeding season in 1991 (Mar-Apr), and presumably they continued to decline for the rest of the study. I believe that hare density in fall 1990 was much higher than the mean reported for 1990-91. This implies the peak and decline were more abrupt than depicted in Figure I-1 which is consistent with other more detailed studies of cyclic hare populations (see Krebs et al. 1986:978). Other researchers have noted that hares begin to crash in winter (Keith and Windberg 1978, Krebs et al. 1986), and there were severe cold spells in November and December 1990 which may have initiated the decline. The seemingly modest increase in density for 1990-91 is explained by a peak and decline in the same year. In summary hare numbers were increasing the year before I began to study lynx reproduction (1989). In the first year of this study (1990) hare numbers peaked over the summer and then declined during the winter. The second year (1991) and third year (1992) of this study hare populations were declining.

Generally hare densities at Snafu were between the peak densities reported for Rochester, Alberta (8.9 hares/ha) and Kluane Lake, Yukon (3.5 hares/ha: Krebs et al. 1986:978). However densities from pellet counts are mean yearly densities while the Rochester and Kluane estimates come from mark-recapture. I assume the peak density at Snafu was higher than the mean density for 1990-91 (7.3 hares/ha) hence the peak Snafu density would have exceeded peak densities at Rochester or Kluane, perhaps considerably. I conclude that the Snafu area was high quality hare habitat probably because of the regenerating forest.

I.6.2. Pregnancy rate

In utero pregnancy rates have been shown to decline with hare density (Brand and Keith 1979, Parker et al. 1983, O'Connor 1984, Poole 1992) and yearlings have often been reported to have lower pregnancy rates than adults (Table I-6). Results from this study generally concur with both of these observations however I do not know if the decrease in birth rate observed during this study was caused by a reduction in pregnancy rate or intra-uterine or post-partum loss of young. Radio locations of females that did not have litters in mid-June suggest some of these females gave birth and lost their litter shortly afterwards. Further results from this study do not explain why more liberal estimates of pregnancy rate from other studies were lower than the live birth rates reported here. One simple explanation is regional differences in habitat quality but this is not supported by lynx carcass analysis (see Table I-6). Lynx from SW Yukon had similar in utero pregnancy rates to other northern lynx populations. Alternatively transient animals may be more susceptible to capture than residents which could bias pregnancy estimates from carcass collections. Transient females may not reproduce as Knick (1990) proposed for bobcats. Perhaps all females at Snafu gave birth in 1990 because they were residents. One immigrant that died was confirmed barren by examining placental scars. Finally, lower in utero pregnancy rates may be due to fading of placental scars between parturition and capture. Entire sets of recent scars would have to fade enough to get classified as old scars to reduce the pregnancy estimate.

Many studies have reported ovulation and implantation in adult lynx during the low phase of the hare cycle (Brand and Keith 1979, Parker et al. 1983, O'Connor 1984). I located several males and females together in March and April 1992 and all adult animals captured in spring were in breeding condition, yet no litters were produced in June 1992. Why do lynx breed if they cannot raise a litter? The cost of gestation is much lower than lactation (Deag et al. 1988:25) and it may pay females to breed in case their condition improves by the time they give birth. Lynx actively searched out pockets of high hare density in another study in SW Yukon (Ward and Krebs 1985) and if a female finds an area of higher hare density she may be able to support a litter, even though hares are declining elsewhere. In summary, birth rates at Snafu lake were higher than pregnancy rates reported for other lynx populations during hare peaks and lower than other populations during the hare crash (Brand and Keith 1979, O'Connor 1984, Poole 1992).

I.6.3. Litter size

Previous work on litter size has involved counts of corpora lutea or placental scars and many studies have recorded a decline in litter size with hare density (Brand and Keith 1979, O'Connor 1984, Poole 1992). The live litter size of adults declined only slightly from the peak (1990) to the crash year (1991) in this study, and any decrease in 1992 would have had little effect on recruitment because no litters survived past the first week of life. Any decline in yearling litter size was also masked by loss of litters within 3 weeks of birth. I

conclude that changes in litter size have little effect on recruitment in lynx. Most studies also show reduced litter size for yearlings (see Table I-6), and though yearling and adult litter sizes were not statistically different in 1990 I believe they were biologically different. This study reports the highest mean litter sizes to date for adult lynx and they were measured 3 weeks after birth. Either my study area provided exceptional lynx habitat, or placental scar counts have a downward bias. Evidence from Chapter II supports the latter.

I.6.4. Winter litter size

Nellis et al. (1972) reported winter litter size at 3.5 (n = 4) during the first year of a hare increase in Alberta. Presumably all these females were adults. Three years of tracking at low densities revealed no kits in winter but the study population was extremely small (3-11). My results concur with these except that Nellis et al. (1972) observed live kittens in summer during low hare years. This would have been very unlikely on our study area because female lynx lost their litters near birth during this period.

I.6.5. Kitten survival

All kitten mortality documented in this study happened over the summer and fall period. No mortality was documented over the winter (Table I-7). Mortality in lion kittens (*Panthera leo*) was greatest in the first six months of life for 3 study areas in East Africa (Packer et al. 1988). Over half the kittens of feral domestic cat population on Macquarie Island were lost before 6 months of age (Brothers et al. 1985).

In 1990-91 yearlings lost their entire litter more often than adult lynx and survival of kittens from yearling females was markedly reduced though sample sizes were low (Table I-7). Why did yearlings have such poor kitten survival in 1990 when hares were abundant? Yearling females may have spent less time with their kittens, or their kittens may have become independent earlier in the winter; both would reduce track count estimates. This is unlikely because 3 new yearling females had litters and I regularly tracked the groups together until spring. Yearling litters were tagged as early as one day old, perhaps this caused abandonment. Radio locations for 2 females with litters that had zero survival in 1990, indicated the mother returned to the nestsite for at least five weeks after tagging. This concurs with behaviour for other females that did not lose their litter. Females may begin to move their litters from the natal den at this time, as do bobcats (Bailey 1979, Wassmer et al. 1988).

It is possible that yearlings were not skilful enough hunters to meet the increased energetic demand of lactation. Female domestic cats utilize their body fat during lactation and smaller cats are more likely to exhibit food stress than larger ones (Deag et al. 1988:35). Yearling lynx are about 2/3 of adult weight (Slough and Mowat, unpubl. data) and have lower body fat than adults (Brand and Keith 1979:835, Parker et al. 1983:776). These physical limitations may translate into lower kitten survival. Finally the observation from cat owners (see Deag et al. 1988:33-34) and lynx ranchers (Alison Tokarchuk-pers. commun.) that yearlings and primiparous females are simply poorer mothers cannot be ruled out as the cause of poor survival.

Yearlings appear more sensitive to prey abundance than adults because kitten survival from yearlings was nearly zero after the hare crash, while survival from adults was the same as the previous year (Table I-7). Hare densities were similar in 1989-90 and 1991-92, yet recruitment was high in the former year and zero in the latter. Lynx and other predators were probably much more abundant in 1991-92 making competition for hares more intense.

I can compare my estimates of recruitment to those from Brand and Keith's (1979) model of the Alberta lynx population for the decline year only. They estimated the reproductive increase to be 2.4 kittens per lynx and kitten survival at 0.35 for a decline year (2 years after the hare peak). Using these figures and assuming an equal adult sex ratio, I calculated fall recruitment to be 1.6 kittens per adult female for the model population. Recruitment ceased entirely in the second year after the hare crash at Snafu which is the appropriate year of comparison.

I.6.6. Snow tracking

My estimates of winter litter size and kitten survival relied on track counts and are subject to the constraints of this method. Sources of error such as kitten independence may have caused an underestimate of litter size. Complete independence in winter would bias counts down but this event was unlikely and was not supported by trapping results, tracking results, or radio locations of kittens. I believe the greatest single bias in track counts was caused by kittens walking in each others tracks and reducing the count. I tried to minimize all biases by repeating counts and combining count data with live-capture results. My winter litter size estimates and birth to winter survival estimates are still likely under estimates.

I.6.7. Litter size, date of birth and kitten sexing

Three litters of seven were located during this study which is previously unreported for lynx. All were born to adults though one female was a two year old that probably did not have kittens the previous winter. Birth weights of a day old litter concur with those reported by Saunders (1961). Another litter located 2-3 days after birth averaged 35 g heavier than the 200 g mean Saunders reported for newborns. Both these litters were from yearlings and newborns of adults may be larger.

The delay observed in yearling parturition could be due to poorer body condition and smaller body size. Alternatively males may select to breed with adult females before yearlings causing a delay in conception. Males would increase their fitness by breeding with adult females first, because the young produced have a greater chance of surviving. One adult female had a litter 4-5 weeks later than normal and at least 5 of these kittens survived until April. This is similar to the period of 44 days required for female bobcats to cycle back into estrus (Crowe 1975), and considerably longer than the period of 15-21 days required for the domestic cat (Asdell 1946:483).

Male kittens tended to be larger than females in 1990 adult litters. In domestic cats the sexes are the same size at birth and males do not grow faster than females until 8 weeks of age (Rosenstein and Berman 1973, Deag et al. 1988:33). Larger body size in bobcats is achieved by an extended period of growth (Crowe 1975), and not by differences in size at birth or growth rate. Perhaps male lynx kittens are able to grow faster than females during periods of super abundance of food. Female lynx were probably in better body condition in 1990 because hares were increasing which allowed male kittens to enjoy faster growth from birth.

Sexing young kittens in the field is reliable though it is more difficult for very young animals. It helps if the litter in hand contains both sexes so the distances between the urinogenital and anal openings can be compared. The single error detected in this study may have been a recording error. Ear-tagging young lynx was a safe and effective way of marking young. This method also works better when kittens are larger because the tag can be placed more easily through a developing cartilage. Smaller tags (size 1 monel) tags were used prior to this study and though sample sizes were small they appeared to come

out more often. Larger tags (size 3) warrant testing because they could be inserted farther into the ears and may stay in better than the ones we used (size 2).

I.7. MANAGEMENT IMPLICATIONS

Extrapolations from this study must first be qualified by defining the population itself. This population was untrapped and the resident female population was stable. No attempt was made to assess recruitment in transient or nomadic animals. One female emigrated during this study, and 3 were killed during live-trapping. Most females studied were known residents; only 2 were suspected immigrants. Reproduction and kitten survival may be different on trapped areas, especially during the decline and low phase of the hare cycle when competition among predators is likely to be more intense. Conversely the recent burn created high quality and continuous hare habitat on the study area. Some south facing slopes had extremely dense stands of regenerating pine that may have provided refuge for hares when predation pressure was intense. These refuges may have provided enough hares to allow adult lynx to reproduce the year after the crash.

Birth rate was defined as the proportion of females with young at about 15 June, not the proportion that actually gave birth to live young. The age at recruitment for lynx is dependent on the hare cycle but can be generalized for high hare years as one year for females and two years for males (McCord and Cardoza 1982:734). This study estimated recruitment to breeding for females and survival to one year for males. A portion of the kitten population emigrated before their first birthday and natural mortality after emigration undoubtedly affected the recruitment rate to the reproductive cohort of male and perhaps female kittens.

1. When hares are increasing, mortality of young between parturition and early winter is the largest factor affecting recruitment because most females breed and give birth. However, during declining hare numbers, recruitment is inhibited by the loss of young before the third week of life. The effect of changes in pregnancy rate and litter size on recruitment could not be assessed during this period.
2. Recruitment by the yearling cohort is negligible during the hare peak. Low recruitment from yearlings would lower the population growth rate significantly, especially during peak years of the hare cycle when yearlings can be up to 50% of the population (Quinn and Parker 1987:691). This would drastically affect recruitment in harvested populations because these populations are made up of mostly young animals (Knick 1990, Garrott and Eberhardt 1987). Recruitment on heavily harvested traplines may be limited to immigration as was found for bobcats in Idaho (Knick 1990:31).
3. Recruitment was high in the year after the hare peak in this population. If this trend is widespread agencies that follow a tracking strategy as proposed by Brand and Keith (1979) would not need to reduce the harvest until at least the second year after the hare peak. By this time there should be few kittens alive in winter and recruitment would be near zero.

Table I-1. Reproductive statistics from lynx litters of radio-collared resident females located in mid-June during a hare peak (1990-91) and decline year (1991-92) in SW Yukon.

	1990						1991		
	ADULTS			YEARLINGS			ADULTS		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
LITTER SIZE	5.3	1.6	12	4.2	0.84	5	4.9	1.1	15
CAPTURE DATE (julian)	165.8	3.4	12	170.0	7.0	5	167.5	3.7	15
MEAN BIRTH DATE	28May		12	14June		4[a]	28May		15
FEMALE KITTEN WEIGHT (g)	610	100	31	239	43.8	11	680	129	31
MALE KITTEN WEIGHT (g)	668	125	32	246	29.6	10	712	152	43
KITTEN WEIGHT (g) both sexes	640	116	63	242	37	21	699	144	74

[a] One female had a late litter (4 July) and was not included in this estimate.

Table I-2. The number of locations of radio-collared kitten lynx that were on and off their mother's home range, in SW Yukon winter 1990-91 and 1991-92. Female home ranges were calculated by minimum convex polygon (100%) using data for a 12 month period 16April-15April and n > 40 in all cases (B. G. Slough unpubl. data). Kitten locations >500 m from the border of the mother's home range were considered off the home range.

	DEC-FEB		MARCH		APR-MAY 15		
Date	On	Off	On	Off	On	Off	Total
90-91	3	0	13	2	9	7	34
91-92	27	3	10	4	17	16	77
Total	30	3	23	6	26	23	111[1]

[1] The proportion of locations on and off the mother's home range differed among the 3 time periods (χ^2=15.04, 2 df, P = 0.001)

Table I-3. Average late-winter litter size for lynx in SW Yukon during a peak (1990-91) and decline year (1991-92) in hare numbers. Litter size was estimated by counting tracks in the snow of females with family groups between late December and March each winter. Resident females were known to be resident for at least one year before they were snow tracked. New females were captured and tracked in the same winter. In 1991-92 estimates for four females that were never captured but were assumed to be resident adults were included in with new females. New females without kittens were excluded.

	1990-91						1991-92					
	ADULTS			YEARLINGS			ADULTS			YEARLINGS		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Resident Females	3.3	1.1	9	0.3	0.58	3	3.8	1.2	8	0.0	0.0	4
New Females	3.3	1.5	3	2.0	1.7	3	3.6	1.1	5	2		1
All Females	3.3	1.2	12	1.2	1.5	6	3.7	1.1	13	0.4	0.89	5

Table I-4. Average number of kittens per female in mid-winter on the Snafu lake study area in SW Yukon during a hare peak (1990-91) and decline year (1991-92). Resident females were known to be resident for at least one year before they were snow tracked. New females were captured and snow tracked in the same winter. Estimates for both groups included counts for females that had no kittens.

	1990-91						1991-92					
	ADULTS			YEARLINGS			ADULTS			YEARLINGS		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Kittens per resident female	3.3	1.1	9	0.3	0.58	3	3.0	1.9	10	0.0	0.0	4
Kittens per new female	2.0	2.1	5	2.0	1.7	3	3.6	1.1	5	2		1
Kittens per female (all females)	2.9	1.6	14	1.2	1.5	6	3.2	1.7	15	0.4	0.89	5

Table I-5. Minimum survival of lynx kittens and litters on the Snufu lake study area in SW Yukon during hare peak (1990-91) and decline years (1991-92). Survival was calculated from capture in mid-June to mid-winter. Kitten survival was calculated using kittens in litters which were counted in winter. Litter survival was the ratio of mid-winter litter size (Table I-3) to spring litter size (Table I-1).

	1990-91						1991-92		
	ADULTS			YEARLINGS			ADULTS		
	$\bar{x}$	CI	n	$\bar{x}$	CI	n	$\bar{x}$	CI	n
Survival of marked kittens	0.66	0.49[a] 0.80	38	0.08	0.00[a] 0.38	12	0.83	0.67[a] 0.94	36
Kitten survival based on average litter sizes	0.63		12/12[b]	0.26		6/5[b]	0.75		13/15[b]

[a] Upper and lower binomial confidence interval (95%)

[b] The first sample size was for the winter litter size (Table I-3) and the second was for the spring litter size (Table I-1).

Table I-6. Pregnancy rate and litter size for selected North American lynx populations at the cyclic peak. I used data described by authors as from years of hare abundance, or I summarized data for any of the 3 years before the hare crash excluding the crash year. Pregnancy and litter size come from presence or absence, and the number of recent placental scars. I assume litter size was calculated for pregnant animals only but this was not always clearly stated. Methods used to estimate hare abundance methods are abbreviated by : LH=lynx harvest; I assumed hares crashed the year of peak lynx harvest, TQ=trapper questionaire, PC=hare pellet counts.

YEARLINGS				ADULTS				Region	Hare Abundance Method	Source
Pregnancy Rate		Litter Size		Pregnancy Rate		Litter Size				
%	n	$\bar{x}$	n	%	n	$\bar{x}$	n			
						5.0	143	Alaska	LH	Berrie 1973:34
60[a]	335	4.2	431	96[a]	138	5.1	172	Alaska	LH	Nava 1970:55
70[b]	404	4.2	292	76[b]	229	4.9	176	Alaska	TQ	O'Conner 1984:57
64	104	4.1	68	97	29	4.3	28	Western NWT	PC	Poole 1991:10
33	103	3.9	34	86	92	4.3	61	Northern Ontario	TQ	Quinn and Thompson 1987
40	129	3.9	129[c]	73	78	4.6	78[c]	Alberta	TQ	Brand and Keith 1979
70	76	4.3	53	91	53	5.1	48	Southwest Yukon	PC	Slough and Mowat unpubl. data

[a] Pregnancy rates are for females that had corpora lutea and are probably slightly inflated.
[b] Pregnancy rates were corrected for the proportion of females that had corpora lutea.
[c] These sample sizes probably include females that were not pregnant.

Table I-7. Summary of estimates of reproduction and recruitment for lynx during a hare peak (1990-91) and decline (1991-92) year in SW Yukon.

	Proportion females with litters in June	Litter size in June	Proportion females with litters in winter	Litter size in winter	Kitten survival June to winter	Kitten Survival winter to June	Recruitment to first year[a]
Yearlings 1990	1.0	4.2	0.5	1.1	0.08	1.0	0.55
Yearlings 1991	0.0		0.2	0.4			0.08
Yearlings 1992	0.0		0				0.0
Adults 1990	1.0	5.3	0.86	3.3	0.66	1.0	2.8
Adults 1991	0.84	4.9	0.87	3.7	0.83	1.0	3.2
Adults 1992	0.0		0.0				0.0

[a] Recruitment is given per female that was resident on the study area from June to winter. Females that died between mid-June and winter were excluded.

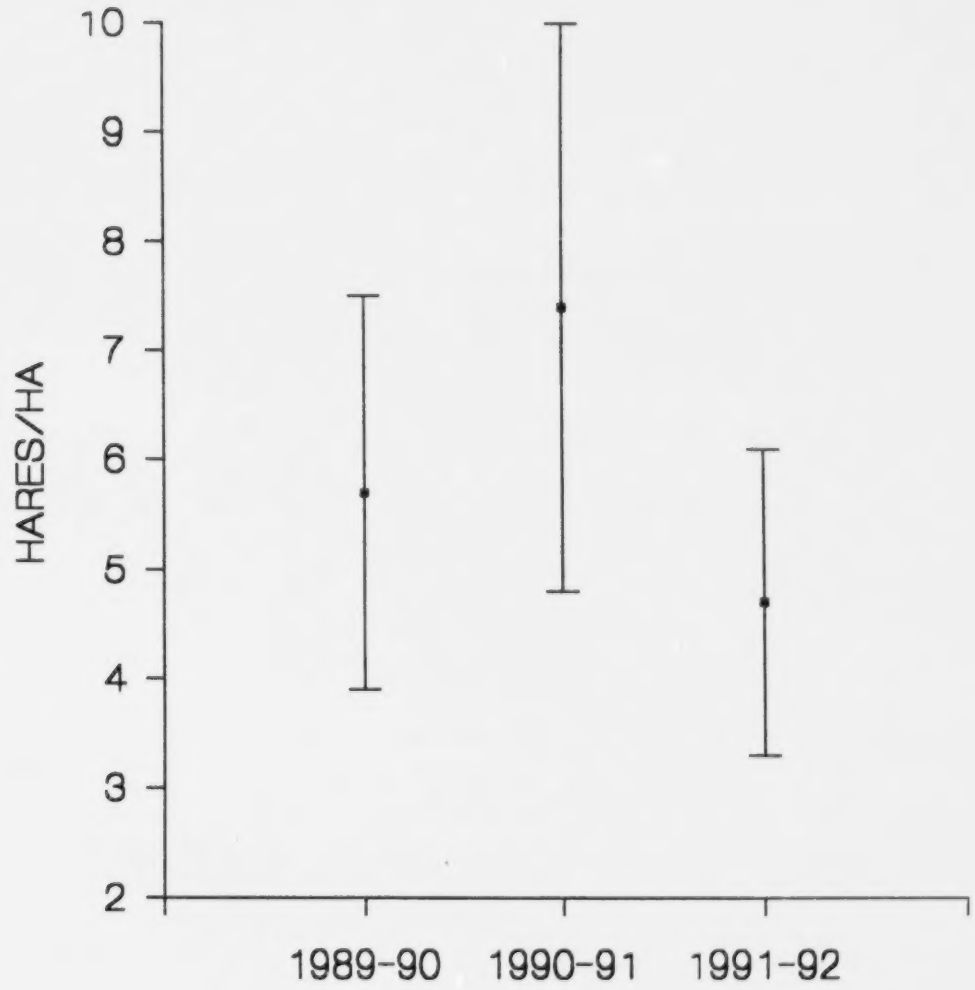


Figure I-1. Snowshoe hare density (hares/ha) for our 282 km^2 study area in SW Yukon. Fecal pellets were counted on 480 quadrants annually. Densities and 95% confidence intervals were predicted from a regression of hare density against pellets/m^2 developed by C. J. Krebs (pers. comm., and see Krebs et al. 1987).

I.8. LITERATURE CITED

Asdell, S. A. 1946. Patterns of mammalian reproduction. Comstock Publ. Co., Ithaca, N. Y. 437pp.

Bailey, T. N. 1979. Den ecology, population parameters and diet of eastern Idaho bobcats. Pages 62-69 *in* P. C. Escherich and L. Blum, eds. Proc. 1979 bobcat research conference. Natl. Wildl. Fed. Sci. and Tech. Ser. 6.

Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40:416-428.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827-849.

Brothers, N. P., I. J. Skira, and G. R. Copson. 1985. Biology of the Feral Cat (*Felis catus* L.) on Macquarie Island. Aust. Wildl. Res. 12:425-436.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester. 234pp.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. J. Mamm. 56(3):177-198.

Deag, J. M., A. Manning, and C. E. Lawrence. 1988. Factors influencing the mother-kitten relationship. Pages 23-39 *in* D. C. Turner and P. Bateson, eds. The domestic cat: the biology of its behaviour. Cambridge Univ. Press, Cambridge.

Garrott, R. A., and L. E. Eberhardt. 1987. Arctic fox. Pages 394-406 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Jackson, D. L. M. 1987. Growth and development of captive bobcats (*Felis rufus*). M. Sc. Thesis, Mississippi State Univ. 63pp.

Keith, L. B. and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildl. Monogr. 58, 1-70.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildl. Monogr. 108,1-42.

Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares.I.Demography of food-supplemented populations in southern Yukon. J. Anim. Ecol. 55:963-982.

Krebs, C. J., B. S. Gilbert, S. Boutin, and R. Boonstra. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565-567.

McCord, C. M., and J. E. Cardoza. 1982. Bobcat and lynx (*Felis rufus* and *F. lynx*). Pages 728-766 *in* J. A. Chapman and G. A. Feldhammer, eds. Wild mammals of North America: biology, management, and economics. John Hopkins Univ. Press, Baltimore, Md.

Nava, J. A. 1970. The reproductive biology of Alaska lynx (*Lynx canadensis*). M. Sc. Thesis., Univ. of Alaska, Fairbanks. 141 pp.

Nellis, C. H., S. P. Whetmore, and L. B. Keith. 1972. Lynx-prey interactions in central Alberta. J. Wildl. Manage. 36:320-329.

O'Connor, R. M. 1984. Population trends, age structure, and reproductive characteristics of female lynx in Alaska, 1961 through 1973. M. Sc. Thesis, Univ. of Alaska, Fairbanks. 111 pp.

Packer, C., L. Herbst, A. E. Pusey, J. D. Bygott, et al. 1988. Reproductive success of lions. Pages 363-383 *in* T. H. Clutton-Brock ed. Reproductive success:studies of individual variation in contrasting breeding systems. Univ. of Chicago Press, Chicago.

Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx on Cape Breton Island. Can. J. Zool. 61:770-786.

Poole, K. G. 1992. Lynx research in the Northwest Territories, 1991-92. Dept. of Ren. Res., Govt. of N.W.T. Manuscript report no. 68. 43pp.

Quinn, N. W. S., and J. E. Thompson. 1987. Dynamics of an exploited Canada lynx population in Ontario. J. Wildl. Manage. 51:297-305.

Quinn, N. W. S., and G. R. Parker. 1987. Lynx. Pages 682-697 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer conservation and management in North America. Ontario Ministry of Natural Resources, Ontario.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

Rosenstein, L., and E. Berman. 1973. Postnatal body weight changes of domestic cats maintained in an outdoor colony. Am. J. Vet. Res. 34:575-577.

Saunders, J. K. 1961. The biology of the Newfoundland lynx, (*Felis canadensis subsolanus* Bangs). Ph. D Thesis, Cornell Univ., Ithaca, N. Y. 109pp.

Saunders, J. K. 1963. Movements and activities of the lynx in Newfoundland. J. Wildl. Manage. 27:390-400.

Slough, B. G., and R. M. P. Ward. 1990. Lynx harvest study 1988/1989. Yukon Fish & Wildl. Branch, unpubl. Progress Report. 79pp.

Ward, R. M. P., and C. J. Krebs. 1985. Behavioral responses of lynx to declining snowshoe hare abundance. Can. J. Zool. 63:2817-2824.

Wassmer, D. A., D. D. Guenther, and J. N. Layne. 1988. Ecology of the bobcat in south-central Florida. Bull. Florida State Mus. Biol. Sci. 33(4):159-228.

CHAPTER II. USING PLACENTAL SCAR COUNTS TO ESTIMATE LITTER SIZE AND PREGNANCY RATE IN LYNX

II.1. INTRODUCTION

Counts of scars on uteri of female mammals are commonly used to estimate litter size and pregnancy rate. Each scar is an implantation site of a fetal placenta on the maternal uterus. This technique is particularly useful for animals that are difficult to observe in the wild. Destructive sampling is required so harvested species have provided convenient samples for study. Reproductive tracts are easy to find and remove, and counting scars does not require special equipment. However several authors have reported placental scar counts overestimate litter size at birth for rats, bobcats (*Felis rufus*), lynx (*Felis lynx*), and raccoons (*Procyon lotor*) (Davis and Emlen 1948, Gashwiler et al. 1961, Beeler 1986, Sanderson 1987). Elder (1952) reported placental scar counts to underestimate litter size at birth for mink. Clearly this method must be tested before using it to estimate litter size or pregnancy rate for a wild population.

Scoring placental scars is easier and faster than counting corpora lutea in ovaries, and requires no preparation of samples. Further, placental scars imply the conception and implantation of young whereas the existence of corpora lutea implies ovulation only (Rolley 1987:672, Quinn and Parker 1987:685). Johnson and Holloran (1985) felt that the number of luteal bodies '*overestimate productivity and do not reflect yearly variation in reproductive effort*'. Numerous authors have reported that counts of corpora lutea were higher than estimates from counting placental scars, embryos, or live young (see tables in McCord and Cardoza 1982:736, Anderson 1987:13). Further estimating the previous year's litter size in North American felids is complicated by the retention of corpora lutea for more than one year (Duke 1949). Not all authors have successfully separated recent corpora lutea from older ones (Brand and Keith 1979, Johnson and Holloran 1985, Knick et al. 1985). Placental scar counts provide the most accurate estimates of reproduction for many species. Counting embryos may provide more accurate reproductive assessment than placental scar counts, but few species are harvested when pregnant.

There is considerable subjectivity in the interpretation of placental scar counts due the possibility of including scars from previous seasons or from aborted embryos. Interpretation may be further complicated by the fading of scars after parturition as reported in foxes (*Vulpes vulpes*) by Lindstrom (1981). Few authors give repeatable descriptions of their methods of interpretation which reduces the comparability and hence, usefulness of results. Bailey (1979) found that placental scar counts in bobcats gave the same litter size he observed in the field. However, he cleared his reproductive tracts which may have reduced scar visibility (see section II.4.1). Macpherson (1969:29) and Lindstrom (1981) compared observations of scars and live litters for individual foxes and found good concordance. Hersteinsson (1984) compared estimates of litter size from counts of placental scars and embryos with those of live litters in arctic foxes (*Alopex lagopus*) in Iceland, and found that live litters were significantly smaller. Gashwiler et al. (1961) found placental scar counts were higher than counts of embryos or live litters in bobcats. Martin et al. (1976) tested placental scar counts against litter size in captive voles (*Microtus ochrogaster*) and found excellent agreement up to 40 days post-partum; scar visibility decreased after 40 days and recovered somewhat after 70 days. Sanderson and Nalbandov (1973) showed that placental scars accurately predicted the number of live young in captive raccoons. Estimates of pregnancy rate from placental scar counts have never been tested against estimates of live birth rate. My objectives in this study were to compare in utero counts of litter size with counts of live litters, and to compare in utero estimates of pregnancy with estimates of birth rate (proportion of females with litters in mid-June) from

observation of live lynx. I review the methods used to score placental scars by other authors. From the above results I recommend a method of classifying placental scars that should provide the most accurate estimates of litter size and pregnancy rate of lynx at birth, and allow more valid comparison of rates among researchers.

II.2. METHODS

Lynx carcasses were collected from fur trappers in southwest Yukon during the winters of 1989-90 to 1991-92. Generally carcasses came from a group of 45 trapping concessions surrounding our lynx study area at Snafu lake in southwest Yukon (see Chapter I). Regenerating boreal forest from the Teslin burn of 1958 covered our Snafu lake study area and parts of 9 surrounding trapping concessions which were located roughly in the middle of the carcass collection area. The remaining 36 concessions were mature boreal forest. In 1989-90, 16 carcasses came from a trapping concession 145 km NW of Snafu lake which was also burned in 1958. Thirteen carcasses came from 2 other concessions that year located 170 km NW of Snafu lake and 170 km east of Snafu lake; both were mature boreal forest. Estimates of pregnancy rate and litter size were collected for adult and yearling lynx from a radio-collared population on the Snafu lake study area (Chapter I).

Lynx were trapped between 1 November and 10 March each winter and the skinned carcasses were submitted frozen. Carcasses were processed throughout the winter and kittens were aged by body size (if <5 kg) or by the open root tip of the canine tooth (for those >5 kg). All other carcasses were aged by cementum analysis of the canine tooth (Brand and Keith 1979, Matson 1981). In 1989-90 and 1990-91 reproductive tracts were removed from thawed carcasses and refrozen in water for later scoring. In 1991-92 uteri were examined the same day carcasses were processed. Many partially rotten carcasses were handled during this study. The uteri of rotten carcasses were often darker and contracted but placental scars were readily visible. No swollen uteri, as seen during estrus, were found in this study (Crowe 1975). Nava (1970) found uteri of lynx in Alaska began to show signs of estrus in late March which is several weeks after the trapping season closed in Yukon.

Reproductive tracts were soaked in water for at least one hour to remove bloodstains from the surface of the uteri. Uteri were split and examined for placental scars over a light source. A glass table with mobile lamps above and below the surface proved most efficient for examining reproductive tracts. Scars were identified as 1 cm wide bands across the uterus and were often surrounded by areas of lighter scarring which faded as distance from the band increased. This diffuse scarring often ran into the diffuse scarring from the adjacent scar, covering much of the uteri. Scars varied greatly in shade from dark black to light brown.

Reproductive tracts from 62 lynx carcasses >1 year old were scored in 1989-90. Scars were graded subjectively as either dark or light. In 1990-91, scars on 68 yearling and adult (>2 years old) reproductive tracts were subjectively scored as dark, medium, or light. In 1991-92, 109 tracts were examined and scars were put into 6 classes based on scar shade after Englund 1970 (or see Lindstrom 1981). Light scars from 1989-90 and 1990-91 were equated to shade 1 scars from 1991-92 and the term *light scars* refers to all 3 groups in this paper. Medium scars from 1990-91 were equated to shade 2 scars from 1991-92 and *medium scars* refers to these 2 groups hereafter. Dark scars from 1989-90 and 1990-91 were equated to the combined categories of shades 3-6 for 1991-92; *dark scars* refers to these 3 groups hereafter. Occasionally scars were grouped into just dark and light categories for analysis; medium scars were combined with dark scars in this case. Note that the scoring of scars was subjective in 1989-90 and 1990-91 but was standardized after Englund (1970) in 1991-92.

Lynx deposit the first cementum layer on their teeth during their

second winter; when they are yearlings (Crowe 1975). Animals with a closed root tip and no annuli are almost certain to be yearlings, but animals with one annulus could be yearlings or two years old. Animals with one annulus were aged by comparing the distance between the annulus and the periodontal interface (Brand and Keith 1979). The possibility of ageing errors could be important in this study because yearling and adult lynx have markedly different reproductive rates (Chapter I).

In utero litter size was estimated by the number of placental scars of a designated shade or darker. The pregnancy rate was the proportion of females with placental scars of a designated shade or darker. In utero litter size was compared to post-partum estimates of litter size for adult lynx in 1990 and 1991, and for yearlings in 1990 (Chapter I). Pregnancy rate was compared to birth rate (proportion of females with a litter in mid-June) for adults and yearlings in 1990 through 1991 (Chapter I). I assumed live litter size and birth rate were the same in 1989 and 1990. Two radio-collared females who's litters were counted in spring were trapped the following winter, and their uteri scored.

II.3. RESULTS

II.3.1. Does Refreezing of Uteri Affect Scar Shade?

To test this question I compared the distribution of scars by shade for 1990-91, when scars were refrozen, and 1991-92, when uteri were examined when removed. There was no difference in the occurrence of scars among shades these two years (χ^2 = 0.995, $\underline{n}$ = 189, 2 df, $\underline{P}$ = 0.61). Twelve uteri from 1991-92 were reexamined after having been frozen six months. Twelve of 50 scars were classified differently from the previous scoring: 7 were higher by one shade, and 5 were lower by one shade. Frozen uteri were re-inspected for classroom demonstrations up to 2 years later with similar results to the first inspection. However scars were very faded in a group of uteri that had become desiccated. In summary, refreezing of uteri did not affect the shade of scars found on those uteri.

II.3.2. Variation in Scar Shade Within Litters

I investigated the variation in scar shade to identify which shades of scars can represent live young. One study area female had four kittens in mid-June and 1 dark and 4 medium scars; at least 3 medium scars must have represented live young (Table II-1). Yearlings had scars of all shades: 38% of 94 yearlings with scars contained light scars, and 31% of 61 yearlings contained medium scars. The distribution of scars by shade was similar for pregnant adults and yearlings for all 3 years studied (Figure II-1). These lighter scars found in yearlings must have been either live or resorbed embryos because they could not have been from the previous year. I observed scars that were dark on one side of the uteri and faded to indistinct on the other, suggesting scars may be different shades at inception or may fade differentially. Placental scars in lynx appear to be lighter than in the fox where scars of shade 5 and 6 were most common (Englund 1970, Harris 1979, Lindstrom 1981); shades 3 and 4 were the most common in this study.

It is unlikely that many of the light scars in adults were from previous litters because this does not explain their occurrence in yearlings. I observed light brown scars located within 2 cm of darker scars but I did not observe 2 similar coloured scars <2 cm apart. I also saw places where a very faint outline of an old scar was apparent under new scarring. I will call these presumably older scars *residual scars* hereafter. Residual scars were far out numbered by other light scars. Lynx placental scars vary greatly in shade and both medium and dark scars can represent live young. The persistence of placental scars for >1 year was uncommon in this sample.

II.3.3. Intra-uterine Mortality of Young

Fetal abortions that leave scars would cause an over-estimate of litter size at birth, and if entire litters are aborted an over-estimate of pregnancy rate as well. Placental scar counts of two females with known litter size both exceeded counts done in the field by one (Table II-1). Neither litter was counted at birth so mortality could have been intra-uterine or post-partum. A crude estimate of intra-uterine mortality can be made by assuming all light scars were a result of in-utero loss. Light scars occurred more frequently in 1991-92, especially in yearlings, concurrent with a decline in hare numbers (Figure II-2). The proportion of lynx with light scars changed little through this study (Figure II-1).

II.3.4. Do Scars Fade Over the Trapping Season?

Most carcasses were trapped December through February (Figure II-3). Litter size was regressed on date of capture to test the hypothesis that the number of scars per female declined through the winter. Light scars were excluded as were females without scars. There was no indication that litter size changed with date of capture for either sex in any year.

If scars faded through the capture period I expect light scars to increase and dark scars to decline in proportion with date of capture. Figure II-4 shows the proportion of females showing light and dark scars. No consistent change is seen across 3 periods of capture: November-December, January, and February-March. Contingency analysis of the proportion of females with dark and medium scars indicated there was no change in proportion across these 3 periods of capture (χ^2 = 0.18, n = 172, 2 df, P = 0.91). The proportion of females with light scars did not change over this period either (χ^2 = 0.05, n = 172, 2 df, P = 0.97). In summary, there was no evidence of scars fading during the period of carcass collection in this study.

II.3.5. Litter Size Differences Among Habitats

Litter size was compared for those carcasses collected around our study area with those from >100 km away to test the hypothesis that the 2 populations had different litter sizes. An ANOVA of area by age indicated there was no difference between litter size (with light scars excluded) for the two areas (F = 0.19, 1, 45 df, P = 0.67).

The radio-collared lynx population resided in regenerating boreal forest while most carcasses came from mature boreal forest. I tested whether litter size was different between forest types by using ANOVA to compare litter size from 9 trapping concessions that were burned in 1958 with the 36 concessions that surrounded the burn area. There was no difference in litter size between areas (F = 0.28, 1, 57 df, P = 0.60) in 1991-92. In 1989-90 and 1990-91 there were only 9 and 12 carcasses respectively for both sexes in the burn; sample sizes were too small for meaningful comparisons.

II.3.6. In Utero vs Post-partum Estimates of Litter Size

Mean in utero litter sizes decreased when lighter shades of scars were excluded for both yearlings and adults (Figures II-5 & II-6). In 1989-90 and 1990-91 no in utero estimates of litter size were significantly different from 1990 live litter sizes regardless of the shade of scars excluded. The mean difference between in utero and post-partum litter sizes was smallest when light scars were excluded: all scars $\bar{x}$ = 0.33, n = 4, light scars excluded $\bar{x}$ = 0.11, n = 4, light and

medium scars excluded $\bar{x}$ = 0.33, n = 2. For adults in 1991, litter size with all scars was not significantly different from the post-partum litter size for that year (t = -1.18, 46 df, P = 0.24). Estimates that excluded light, and light and medium scars were both significantly lower than the live litter size that year (t = -2.09, 42 df, P = 0.04 and t = -2.77, 39 df, P = 0.009 respectively). In utero estimates correctly predicted a decline in litter size for adults in 1991-92, though the decline was greater than that seen in the field (Figure II-5). Note the decline in adult post-partum litter size from 1990 to 1991 was not significant (see Section I.5.3). In summary, medium and dark scars best predicted live litter size in 1989-90 and 1990-91 but all scars best predicted litter size for adults in 1991.

II.3.7. Pregnancy Rates vs Birth Rates

Birth rates from the field were in best accordance with pregnancy rates when all 3 scar shades were included, and yearling in utero rates were still consistently lower than the live birth rate in 1990 (Figures II-7 & II-8). The decline in adult birth rate in 1991-92 was accurately predicted by pregnancy rate estimates. However pregnancy rates for yearlings in 1991-92 considerably over-estimated the live birth rate, because all yearling litters were lost at birth (Chapter I).

II.3.8. Effects of Ageing Lynx on Litter Size

To remove the effect of incorrect ageing, all placental scar counts were pooled and compared to a pooled estimate of litter size in the field. This comparison was made for 1990-91 because it was the only year I had counts for both adult and yearling litters from the field. The proportion of yearlings (estimated by cementum analysis) was similar in the trapped sample and in our radio-collared sample of females (0.42 and 0.45). The in utero estimate was 5.2 ± 1.54 (SD: n = 56) when all scars were included and 4.9 ± 1.25 (n = 52) when light scars were excluded. The pooled mean litter size from field observation was also 4.9 ± 1.48 (n = 17).

II.4. DISCUSSION

II.4.1. Handling of Uteri

The handling of carcasses and uteri necessarily affects placental scar counts. In the north, trappers must often keep their carcasses the entire winter because of the remoteness of many traplines. Most carcasses are stored outdoors and thawing and desiccation are bound to cause deterioration. Few carcasses are not somewhat *blue* in the abdominal cavity; often this happens while thawing for processing. These carcasses have placental scars but deterioration of abdominal contents may cause some the reported variation in scar coloration and warrants investigation. Nava (1970) reported using seriously desiccated carcasses in his sample though he did not say if this had any noticeable affect on the colour of placental scars. I conclude that refreezing of uteri for up to six months does not affect scar coloration. This is consistent with the conclusion of Lindstrom (1981) for foxes.

Uteri were soaked in water before examination during this study. Nellis et al. (1972) reported that scars were faint after clearing, and several authors have reported the fading or complete disappearance of scars due to fixing in alcohol or formalin (Saunders 1961, van Zyll de Jong 1961, Lloyd as cited in Englund 1970, Nellis et al. 1972, Stewart 1973). Mech (1980) fixed entire reproductive tracts and found scars on only 2 of 22 sets of uteri, which he attributed to low breeding frequency. Bailey (1979) cleared reproductive tracts for bobcats and he cited '*study techniques*' as one possible explanation for the low

proportion of females showing placental scars. However Brand and Keith (1979) fixed tracts in 10% formalin and successfully counted placental scars. Martin et al. (1976) analyzed the effects of both clearing and fixing on vole uteri and found no technique was clearly superior to fresh uteri. They said, '*After a few weeks post-partum, fixation, and/or clearing will improve contrast and cell density for visualization of superficial small scars*' (Martin et al. 1976:269). Gilbert (1987) recommends two methods of tissue preparation to enhance the visibility of placental scars but does not comment on their benefits in comparison to using fresh uteri. Fixing or clearing may help the observer to see very light scars though the only evidence to support this comes from voles; the above studies do not support their usefulness in lynx. Further, the extra time involved in preparation of samples may not be warranted, especially if lighter scars are excluded for estimation of litter size.

II.4.2. Variation in Scar Shades Within Litters

Medium and dark scars can represent live young which implies a system is needed to separate them from other possibly non-fertile scars. Observations from F15, a study area female, show that at least 3 kittens resulted from medium scars. Many medium scars must have represented live young because the large disparity between in utero and live litter sizes caused by excluding light and medium scars from in utero estimates is unrealistic (Figures II-5 and II-6). The question of whether light scars can represent live young, or whether all medium and dark scars represent live young cannot be answered without further uteri from females with known litter size. Lindstrom (1981) found that lighter scars represented viable implantation sites in foxes with known litter sizes (and see Table 13 in Macpherson 1969:29). Martin et al. (1976) found that retention of scars can vary within a litter, and within a species. They quote four extreme cases where recently parous females had no placental scars at all. Both Lindstrom (1981) and Martin et al. (1976) found considerable variation in scar shades within a litter, as was found in this study.

Few placental scars persist more than one year in lynx because there were similar numbers of light scars in adults and yearlings. Some residual scars may be subjectively separated from other light scars. Light scars that are <2 cm from a darker scar or covered by diffuse scaring from a darker scar could be recorded separately to confirm the occurrence of a previous litter. The number of other light scars may then more accurately reflect the rate of resorption loss.

Foxes, raccoons and voles have been shown to retain scars through a breeding cycle (Macpherson 1969, Englund 1970, Sanderson and Nalbandov 1973, Martin et al. 1976, Lindstrom 1981). I believe few residual scars appear in lynx because diffuse scarring around implantation sites combined with large litter sizes covers scars from previous pregnancies. Martin et al. (1976) showed that old scars in voles had retreated deeper into the muscle of the uterus, hence new scarring on the surface of the uterus would cover an old scar.

II.4.3. Intra-uterine Mortality of Young

Intra-uterine mortality was not confirmed in this study, however there was circumstantial evidence for its occurrence. Two females had one less live kitten than predicted by placental scars. Whether these kittens were lost before or after birth is unknown. One radio-collared female located shortly after birth had a stillborn kitten (Chapter I) which shows immediate post-parturition loss does occur. The number of light scars is a crude estimate of non-fertile sites in this sample because residual scars were few. Light scars were 18% of all scars in 1989-90, 16% in 1990-91, and 26% in 1991-92 (see Figure II-2 for

proportions by age class). The increase in the proportion of light scars in 1991-92 may be a result of food shortage caused by a declining hare population.

Saunders (1961) found a minimum of 13% post-implantation loss in lynx in Newfoundland. He observed females that were resorbing individual embryos, and one case of an entire litter being resorbed. Intra-uterine mortality occurred at 19% of implantation sites in pregnant foxes (Lindstrom 1981). Englund (1970) did not quantify individual resorption loss in the foxes he studied, he did say 18 of 268 (6.7%) samples experienced complete litter loss, post-implantation. He generally observed complete litter loss before mid-term, but individual resorptions occurred throughout pregnancy. Payne (1984) documented 3% post-implantation loss (resorption) in beaver (*Castor canadensis*) and suggested this figure was a minimum. He felt resorption loss was related to food quality. The crude estimates of in utero mortality in this study were similar to estimates for other medium sized mammals and supported Payne's hypothesis that resorption loss is related to food supply.

It has not been established whether resorbed or aborted embryos produce lighter scars than full-term young. Sanderson and Nalbandov (1973) found resorbed embryos older than 30 days had similar placental scars to those of term young in raccoons, and these persisted for at least 10 months. Conaway (1955) found that embryos aborted after 11 days left similar coloured scars to term young in laboratory rats. Macpherson (1969), Lindstrom (1981), Sanderson and Nalbandov (1973), and this study all reported females that had 1 more dark scar than live young. If the extra young were aborted they left similar coloured scars to their siblings. Englund (1970) found that pigmented material occurred behind embryos as young as 29 days in foxes and suggested they may produce scars at this stage. Gosling (1980) found placental scars in the copyu (*Myocastor coypus*) after 10 days of pregnancy. He separated scars younger than 35 days based on the number of black dots making up the scar. Martin et al. (1976:268) found scars of aborted voles were '*dark and fully formed and contrasted sharply with the newly involuted sites of the term young*' a few days post-partum. The differences between fertile and non-fertile sites may not be discernable several months post-partum. Sanderson and Nalbandov (1973) suggest scars may fade faster in females that abort their entire litter.

II.4.4. Fading of Scars Over the Trapping Season

Support for the fading of scars was not found in this study. The majority of carcasses were collected between December and February and the fading of scars over this period may be too slight to be detected. Nava (1970) found no difference in yearling litter size from November to May as estimated by placental scars, though he did not mention what shade of scars he excluded. Lindstrom (1981) showed that his data, and data he reanalyzed from Englund (1970), supported the hypothesis that scars of foxes fade after parturition. However both these authors collected carcasses over a 7-month period (Sept-Mar). Johnson and Holloran (1985) looked at the proportion of barren females by two week periods in bobcats and found no trend in pregnancy rate with date. They concluded scars did not fade over their 2 month collection period (Dec-Jan). Martin et al. (1976) found that vole scars faded between 40 and 80 days post-partum but were visible again after this period until at least 200 days post-partum. I conclude the fading of scars contributes little error when estimating litter size or pregnancy rate if carcasses are collected over <3 months.

II.4.5. What Scars to Use to Estimate Litter Size and Pregnancy rate

Results from this study suggest that placental scar counts best

predict post-partum litter size when light scars are excluded from the counts. This assumes that litter size was the same in the trapped sample and the radio-collared population in 1989-90 and 1990-91. There are 5 reasons why the most accurate estimates of reproduction are probably achieved when light scars are excluded:

1. In utero litter sizes were closest to post-partum litter size when light scars were excluded in 1989-90 and 1990-91.
2. In utero litter sizes were closest to post-partum litter size when all scars were included in 1991-92, but litter size may have been different between the Snafu lake study area and the trapped sample due to the decline in the hare population.
3. Pregnancy rates were closest to live birth rates when all scars were included but litter size was more likely to have been the same in the radio-collared and trapped populations than pregnancy rates.
4. Given the evidence for the occurrence of residual scars and intra-uterine mortality in this and other studies, it is unreasonable to expect all scars represent live young.
5. Excluding light and medium scars gives unreasonably low pregnancy rates and litter sizes. Further medium shade scars can represent live young.

When light scars were excluded in utero litter sizes were generally slightly lower than rates from observation of radio-collared lynx (Figure II-5). Yet live litter sizes were probably conservative due to post-partum mortality between birth and capture (see Chapter I). Why were in-utero litter sizes not higher than live litters? The exclusion of light scars may exclude some fertile scars. Alternatively some scars may have faded prematurely or never formed as Martin et al. (1976) observed for a small portion of vole litters. Sanderson and Nalbandov (1973) report a racoon with 3 live young and only one scar. I observed scars that were dark on one side and light on the other which suggests scars may form or fade differentially. This may be caused by the storage or deterioration of carcasses before handling. This study cannot separate these two possibilities and researchers using placental scar counts for lynx should realize the method I propose may be conservative.

When light scars were excluded the trapped sample had considerably lower pregnancy rates (up to 30%) than the birth rates from the untrapped study area. I chose what shade of scars to include in intra-uterine estimates based solely on litter size because pregnancy rate was more likely to be different between the trapped and radio-collared populations due to differences in residency status. Seidensticker et al. (1973) showed transient cougars (*Felis concolor*) do not breed, Knick (1990) and Bailey (1972) both felt that transient female bobcats may not breed, and circumstantial evidence from Chapter 1 supported this occurrence in lynx. I suggest that transient, and consequentially barren females, are over-sampled in trapped samples which biases the pregnancy rate estimate (see Bailey 1979). This bias is likely to vary with trapping effort, making correction difficult.

If the trapped sample had different mean litter size than the radio-collared sample in 1989-90 and 1990-91, my conclusions as to how to best estimate reproduction are invalid. There are a number of factors that may have caused a difference in litter size between the two populations. Generally, trapped areas should have higher reproduction due to reduced competition for food. However, during the peak years of the hare cycle food is unlikely to be limiting for any lynx population. Litter size is unlikely to vary among populations as long as individuals have similar levels of food. The trapped population generally came from mature boreal forest, which was probably lower quality hare habitat relative to the regenerating habitat the radio-collared lynx lived in. Comparison of litter size between regenerating and mature forest areas indicated no difference between the two habitat types. Trapped populations have lower mean ages than untrapped populations (Rolley 1987:673, Knick 1990). I separated litter size estimates for yearling and >2 year old lynx. Quinn and Thompson (1987) have shown a small

difference in litter size between 2 year old lynx and those >2, but this difference was too small to have caused a reduction in adult litter size in the trapped sample. Trapping itself may affect reproduction by destabilizing social structure (Dyer 1979). This factor is likely to affect residency status and breeding success, and hence pregnancy rate rather than litter size. While differences in litter size among the 2 study populations cannot be ruled out, I submit that assuming litter size was similar is the most parsimonious choice in lieu of other information.

Including all scars in placental scar counts more accurately predicted birth rate in all years, and litter size for adults in 1991. It also slightly overestimated litter size in 1989 and 1990 which is expected because live litter sizes were probably conservative. Including all scars assumes the error due to intra-uterine mortality can be ignored. Evidence from studies of other species such as foxes suggests that intra-uterine mortality occurs at up to 19% of implantation sites. All scars may accurately predict birth rate and litter size because some light scars are fertile sites, or some embryos may not form scars or the scars may fade prematurely. Only the study of female uteri with known litter size can separate these 2 possibilities and confirm whether light scars should be included in placental scar counts.

Have other researchers estimated litter size accurately? This is difficult to answer because few give the criteria they used when deciding which scars to include in their estimates. Table I-6 summarizes litter sizes reported for lynx during the peak phase of the hare cycle. Litter sizes are remarkably constant across regions. Adult and yearling litter sizes averaged 0.55 and 0.14 lower, respectively, than the 1990 live litter sizes from Snafu. However, Snafu litter sizes are likely underestimates of litter size at birth. I infer some researchers may have been subjectively excluding too many scars from placental scar counts.

In utero litter size changed relatively little with food supply. This has been noted for other small felids (Deag et al. 1988). The in utero litter for yearlings was 1 kitten fewer in 1991-92 than the previous year, yet few if any yearlings we able to raise a litter. Similar declines in adult litter size from peak to decline phases of the hare cycle have been noted (Brand and Keith 1979, O'Connor 1984, Poole 1992). Declines in both litter size and pregnancy rate were predicted in utero, however large changes in prey abundance and recruitment were followed by relatively small changes in both litter size and pregnancy rate (Chapter I). Yearling pregnancy rate declined the most when hares crashed and this parameter may be the most sensitive in utero predictor of the hare crash, however changes in trapping pressure may obscure this response. Declines in in utero estimates of reproduction underestimated the decline in recruitment because mortality near birth was an important factor limiting recruitment in lynx (Chapter I).

II.5. SUMMARY AND RECOMMENDATIONS

1. Clearing or fixing of lynx uteri probably does not improve the visibility of placental scars.
2. Refreezing lynx uteri for examination up to six months later does not affect the visibility or the shade of scars.
3. Persistence of scars through more than one year is rare in lynx. Scars that are located <2 cm from a darker scar, or are covered by diffuse scarring from a darker scar, are probably from the previous year and could be recorded as residual scars.
4. Intra-uterine mortality probably contributes a greater error to the estimation of litter size than the retention of scars over more than one year. I suggest light scars represent sites of intra-uterine mortality. However, there is little proof in the literature that aborted embryos produce appreciably lighter scars than full-term young.

5. The fading of scars was not seen in this sample. If carcasses are collected over <3 months, errors caused by fading are probably small.
6. I recommend investigators record placental scars according to 6 shades of darkness as in Englund (1970) and Lindstrom (1981), with a seventh category for residual scars. Separation of darker scars may not be necessary (shades 3-6 in Englund 1970) but further study may demonstrate their utility. For example, it may be shown that when scars in the same litter are separated by more than 2 categories the lighter scars are aborted young. These methods will allow more rigorous comparison of rates among studies, and the correction of estimates from previous studies if and when a more rigorous test of the technique is done.
7. For lynx, the most accurate estimate of live litter size and birth rate is probably attained by excluding light scars (Shade 1 scars from Englund 1970).
8. In utero estimates of pregnancy rate should be used carefully to estimate birth rate in the sample population. Trapped samples may misrepresent reproductive output because barren transients are over-sampled compared to their abundance. This bias probably changes with trapping intensity making correction difficult.
9. During food shortage, in utero pregnancy rates may not accurately predict the number of viable litters produced due to mortality near birth.
10. In utero litter size changes relatively little in lynx, even with massive changes in reproductive output and prey density. Researchers must keep this in mind if litter size is used to predict the crash in hare or lynx populations, or to estimate litter size for population modelling.

Table II-1. Placental scars counts and live litter size for radio-collared female lynx from south west Yukon.

Female	Placental Scars			Number of live young	Age of young (days)
	Dark	Medium	Light		
FNY	6			5	16
F15	1	4		4	4

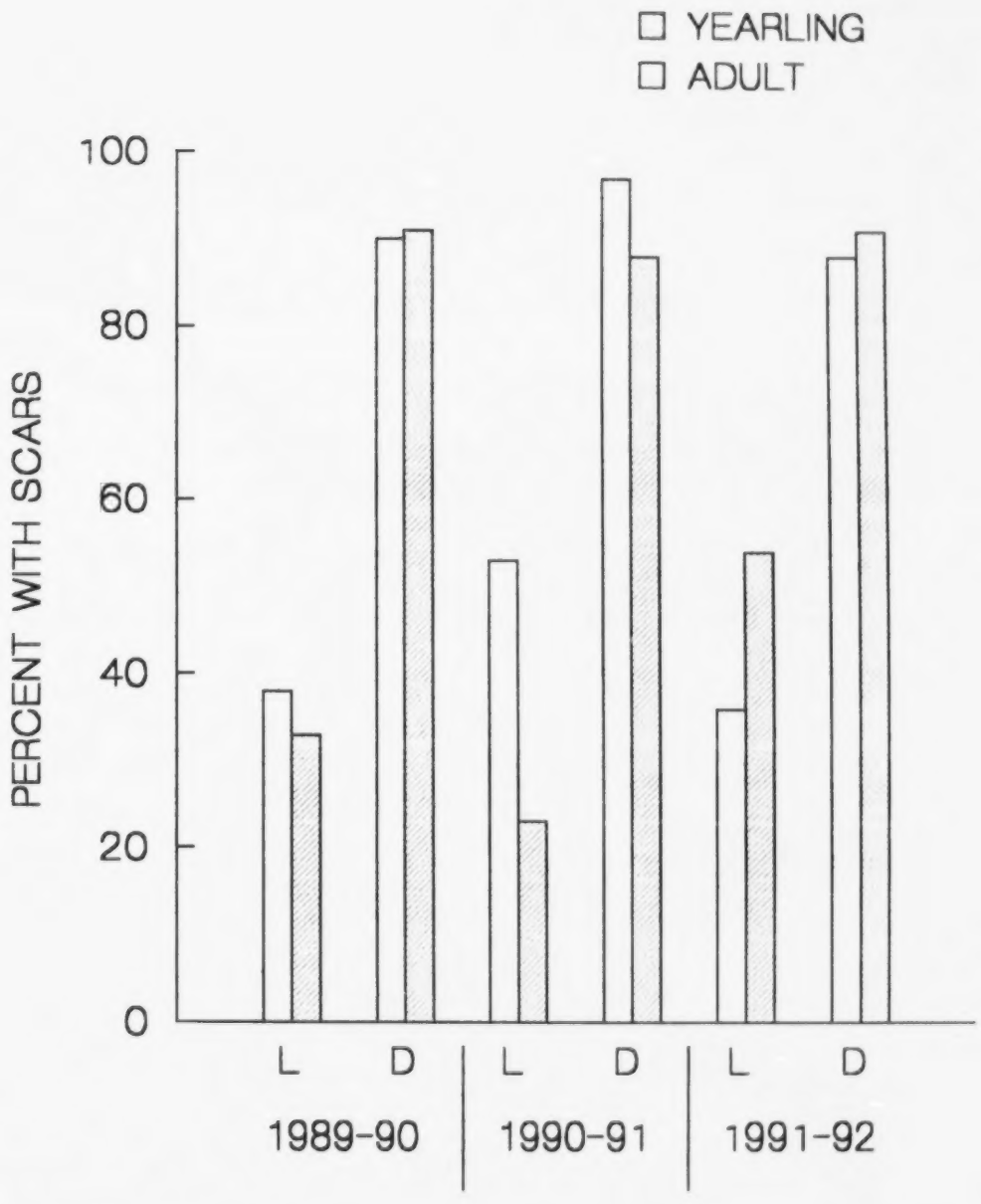


Figure II-1. The proportion of yearling and adult lynx with light and dark placental scars. Uteri without scars were excluded.

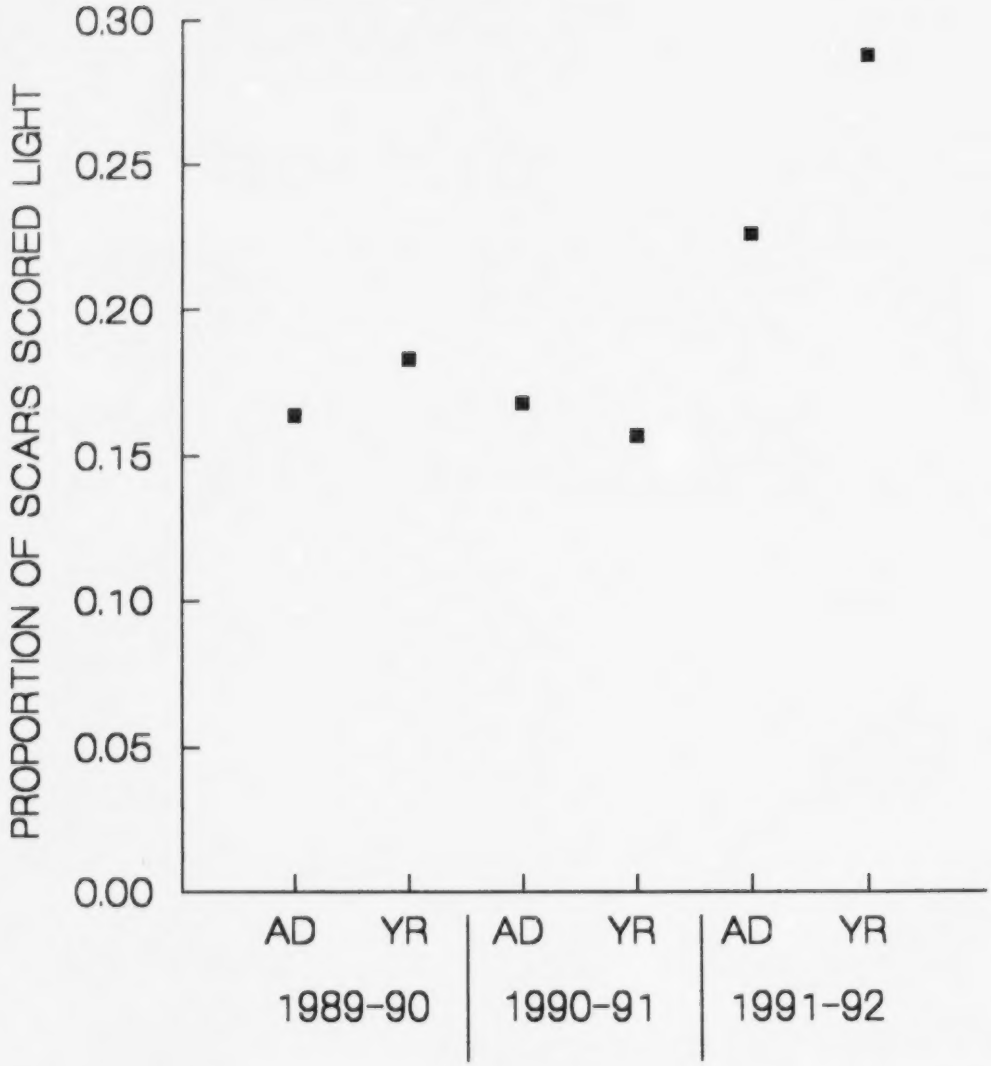


Figure II-2. The proportion placental scars that were scored light on adult and yearling lynx uteri from SW Yukon. Uteri without scars were excluded.

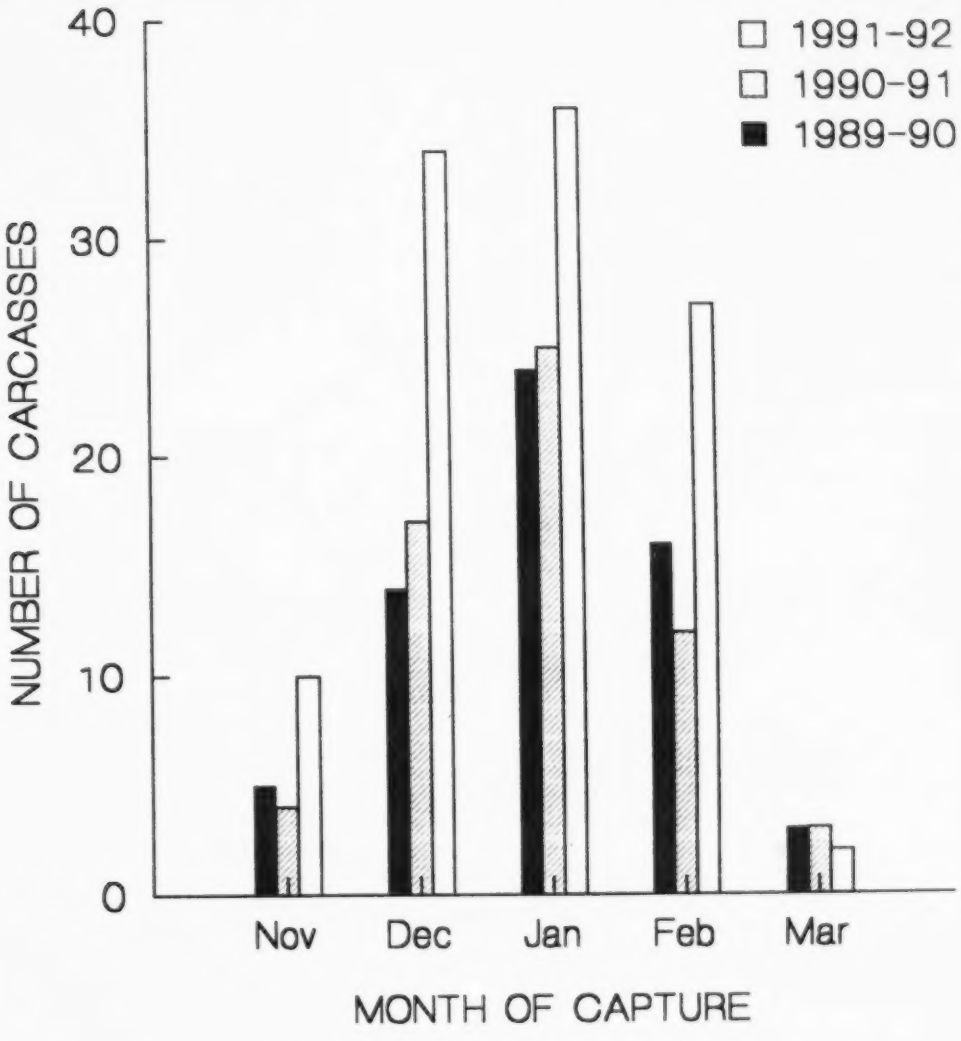


Figure II-3. The number of female lynx carcasses collected per month from fur trappers in SW Yukon between 1989-90 and 1991-92.

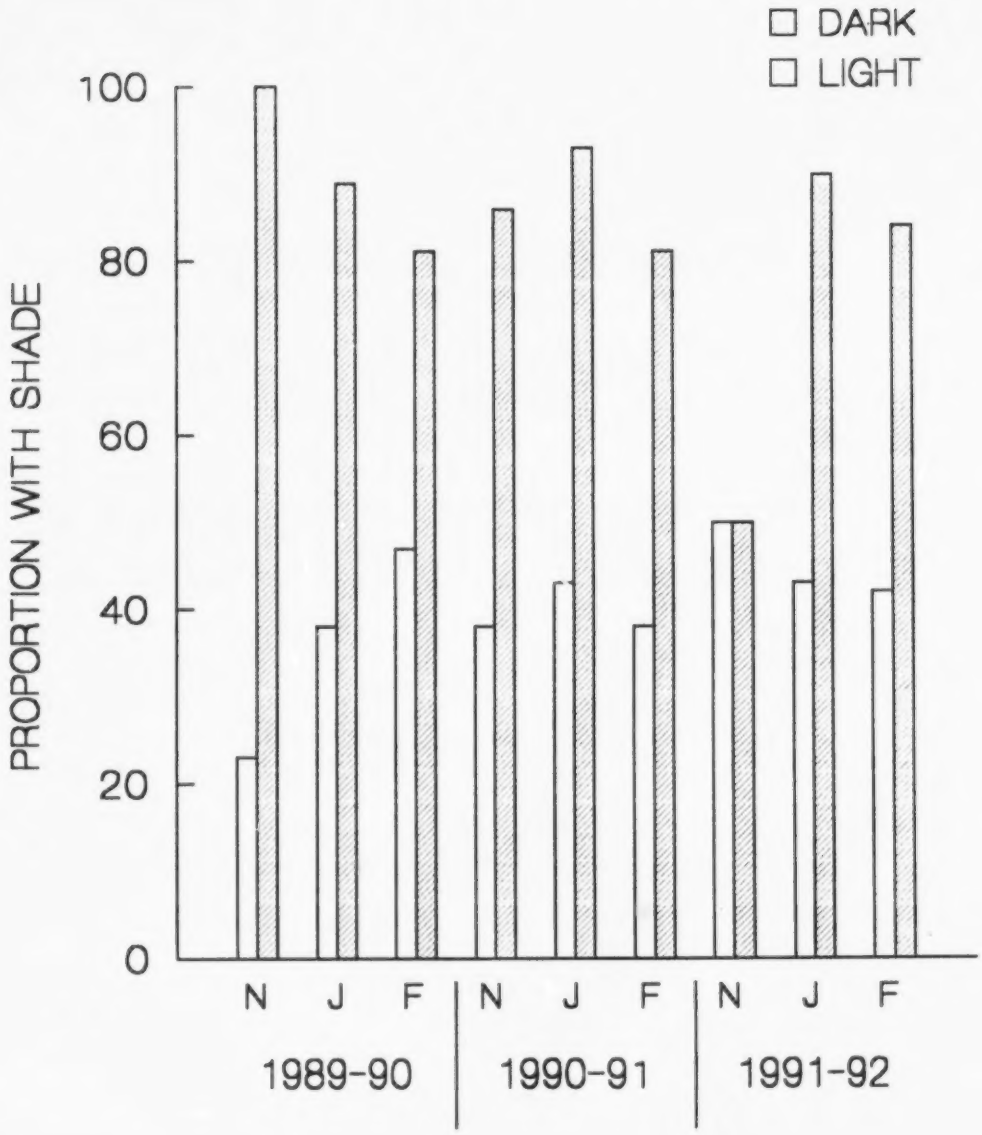


Figure II-4. The proportion of females with light and dark placental scars during 3 periods of harvest (Nov-Dec, Jan, Feb-Mar) for lynx carcasses from SW Yukon, 1989-90 to 1991-92. Females without scars were excluded. Dark and medium categories were combined for 1990-91 and 1991-92.

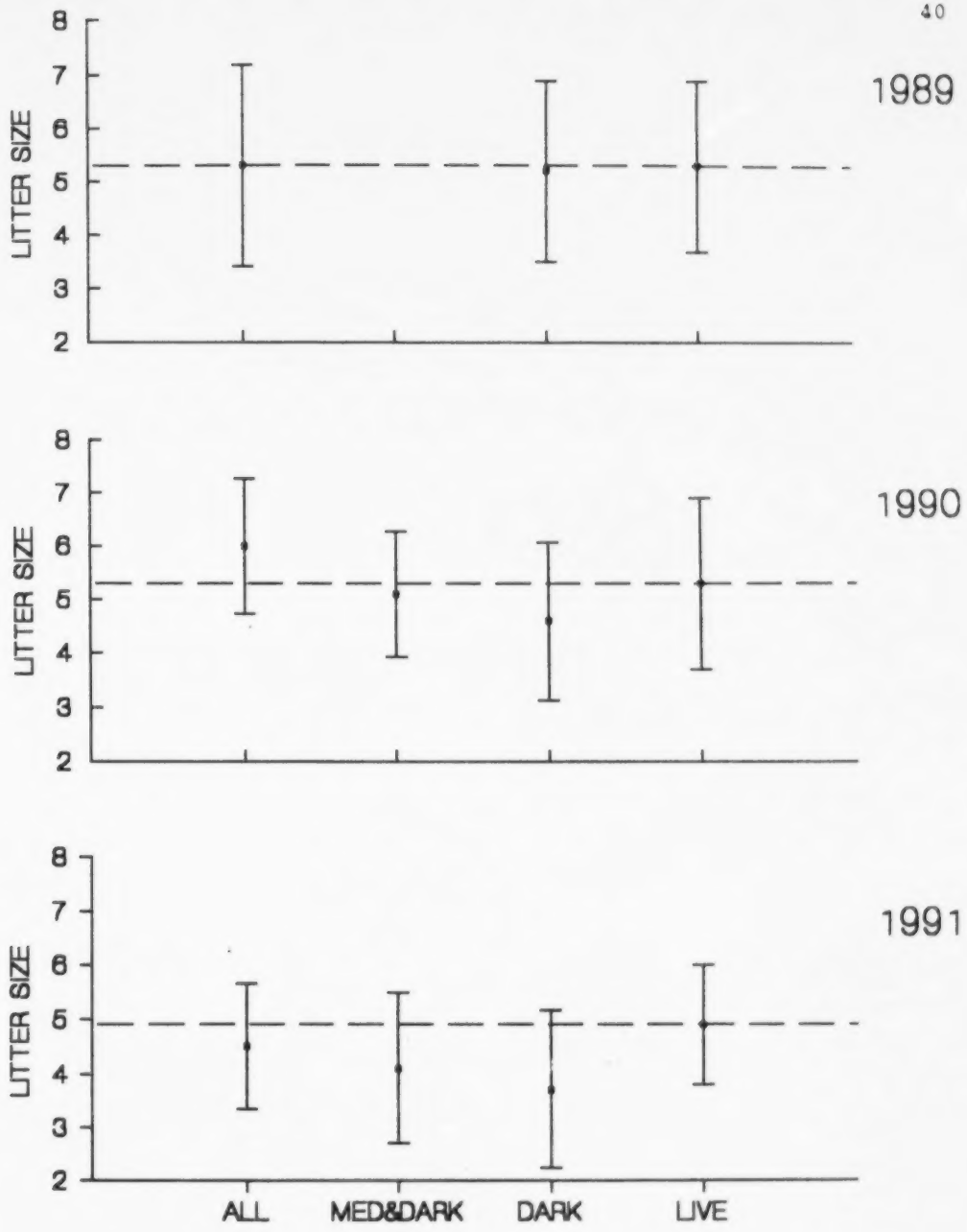


Figure II-5 Litter sizes of adult lynx during 1989-90 to 1991-92 resulting from the combination of placental scars of different shades: ALL = all scars combined, MED&DARK = medium and dark scars combined, DARK = dark scars only. LIVE is the litter size observed post-partum from radio-collared lynx in 1990 and 1991 (Chapter I). Error bars are one standard deviation.

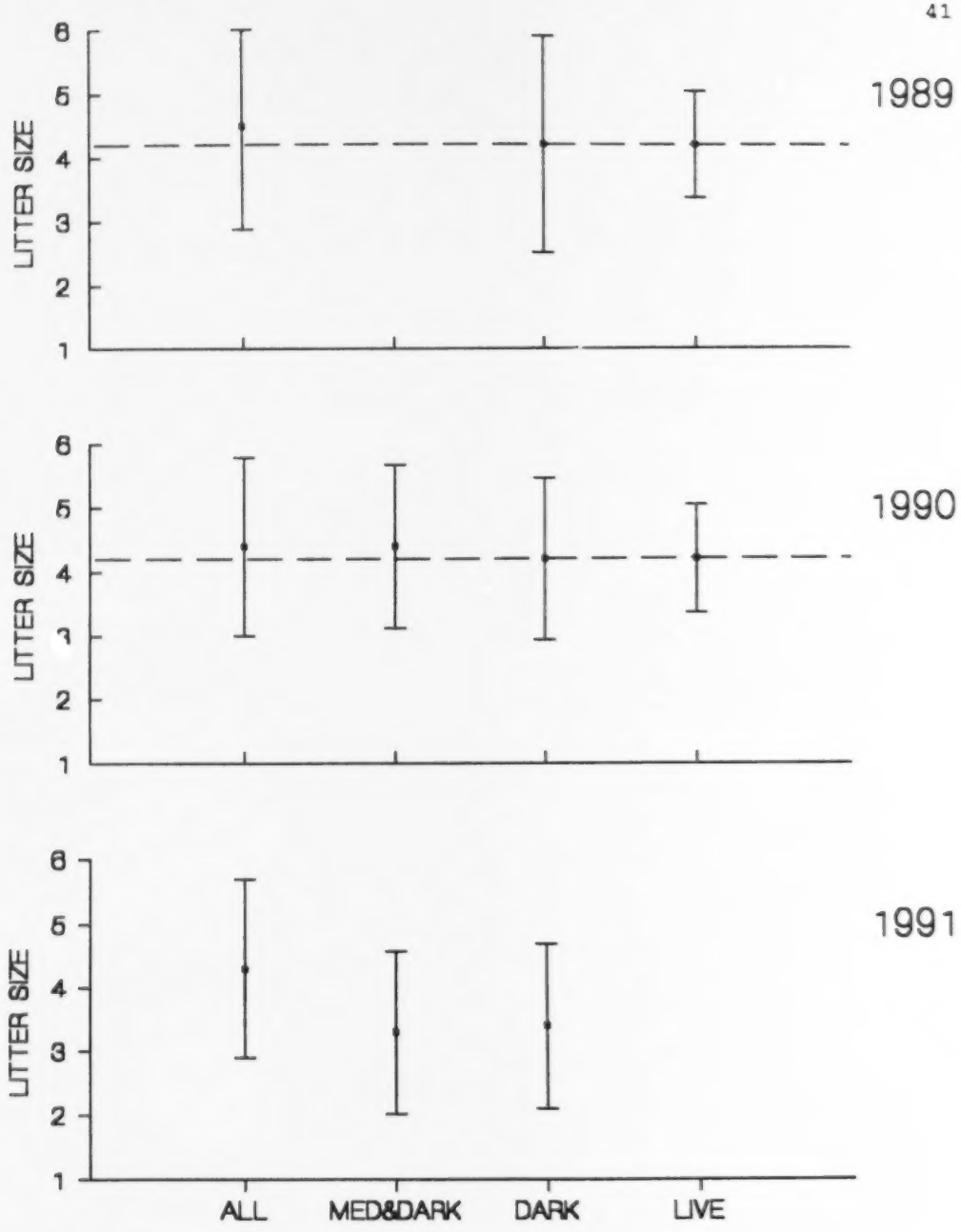


Figure II-6 Litter sizes of yearling lynx during 1989-90 to 1991-92 resulting from the combination of placental scars of different shades: ALL = all scars combined, MED&DARK = medium and dark scars combined, DARK = dark scars only. LIVE is the litter size observed post-partum from radio-collared lynx in 1990 (Chapter I). Error bars are one standard deviation.

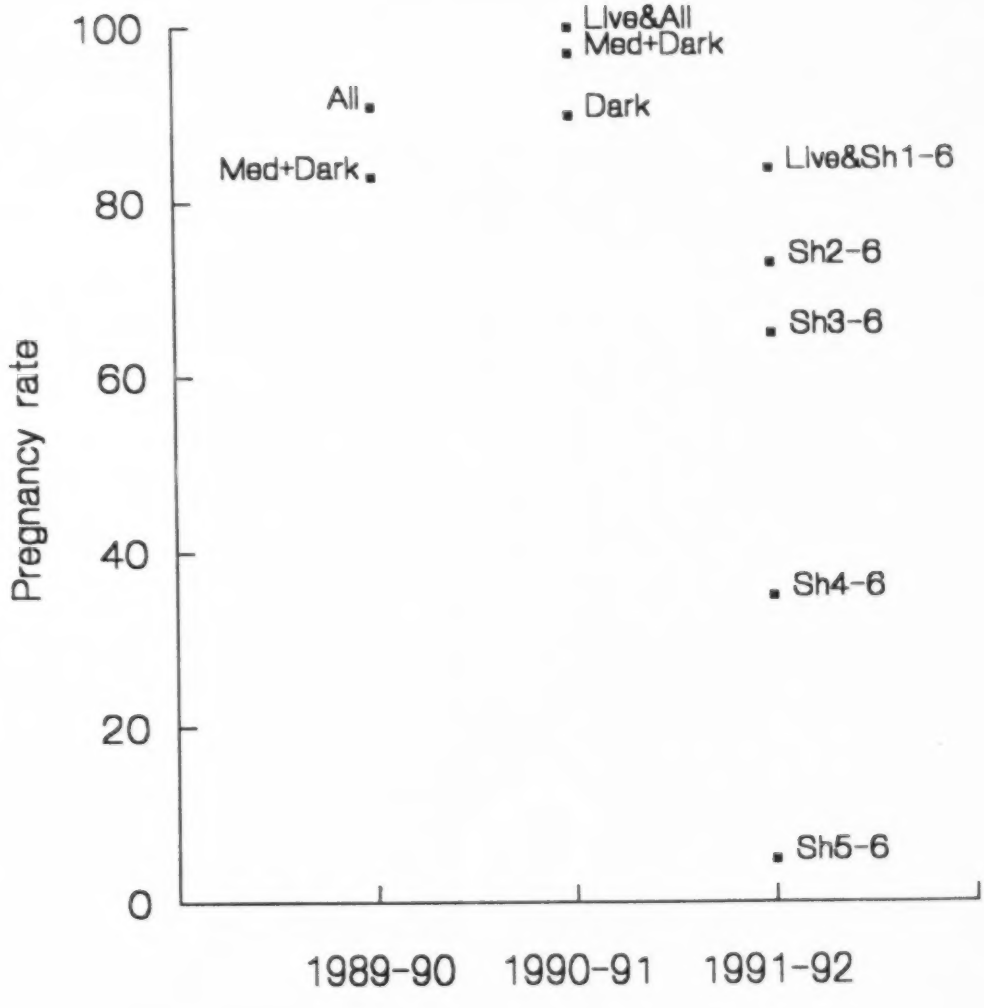


Figure II-7 Pregnancy rates of adult lynx during 1989 to 1991 resulting from the combination of placental scars of different shades: ALL = all scars combined, MED&DARK = medium and dark scars combined, DARK = dark scars only. LIVE is the pregnancy rate observed post-partum from radio-collared lynx in 1990 and 1991 (Chapter I).

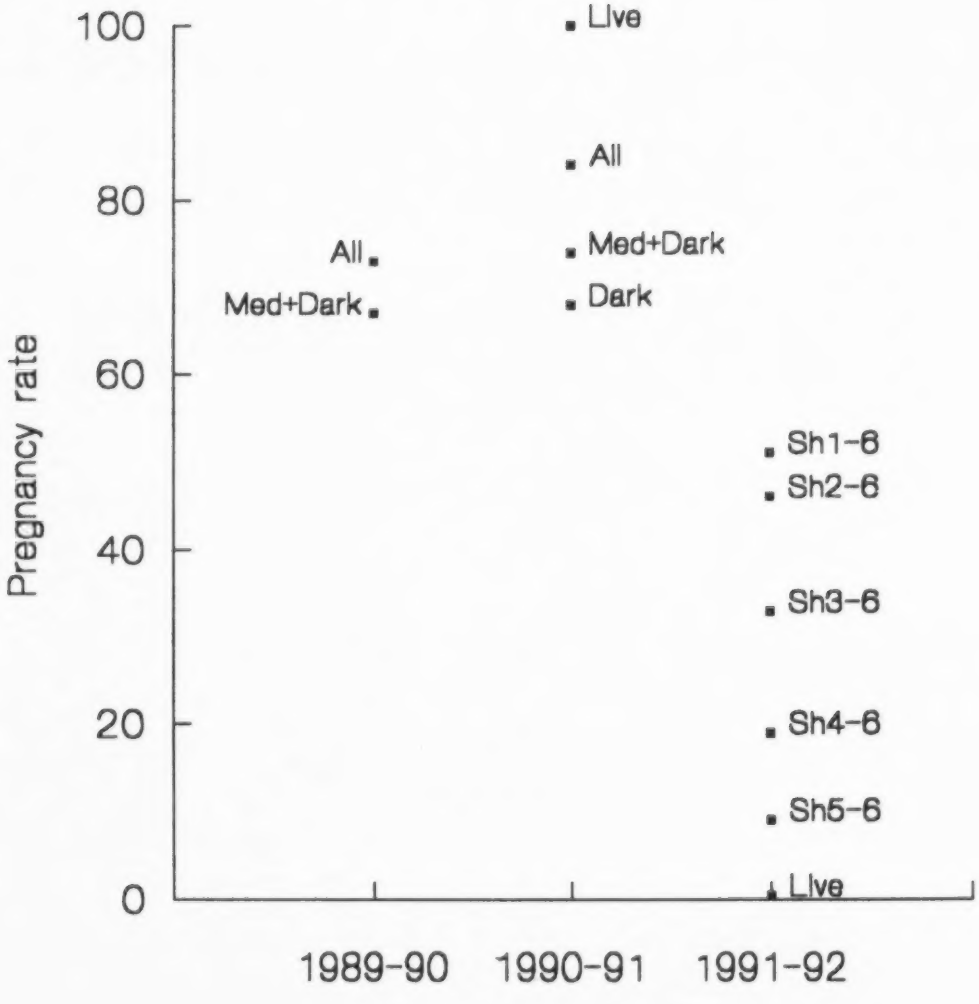


Figure II-8 Pregnancy rates of yearling lynx during 1989 to 1991 resulting from the combination of placental scars of different shades: ALL = all scars combined, MED&DARK = medium and dark scars combined, DARK = dark scars only. LIVE is the pregnancy rate observed post-partum from radio-collared lynx in 1990 and 1991 (Chapter I).

II.6. LITERATURE CITED

Anderson, E. M. 1987. A critical review and annotated bibliography of literature on the bobcat. Colorado Division of Wildlife. Special report no. 62. 68pp.

Bailey, T. N. 1972. Ecology of bobcats with special reference to social organization. Ph. D. Thesis. Univ. Idaho, Moscow. 82pp.

Bailey, T. N. 1979. Den ecology, population parameters and diet of eastern Idaho bobcats. Pages 62-69 *in* P. C. Escherich and L. Blum, eds. Proc. 1979 bobcat research conference. Natl. Wildl. Fed. Sci. and Tech. Ser. 6.

Beeler, I. E. 1986. Reproductive characteristics of captive and wild bobcats in Mississippi. M. Sc. Thesis. Miss. State Univ., Miss. State. 81pp.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827-849.

Conaway, C. H. 1955. Embryo resorption and placental scar formation in the rat. J. Mamm. 36(4):516-532.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. J. Mamm. 56(3):177-198.

Davis, D. E., and J. T. Emlen, Jr. 1948. The placental scar as a measure of fertility in rats. J. Wildl. Manage. 12:162-166.

Duke, K. L. 1949. Some notes on the histology of the ovary of the bobcat (*Lynx*) with special reference to the corpus lutea. Anat. Rec. 103:111-132.

Deag, J. M., A. Manning, and C. E. Lawrence. 1988. Factors influencing the mother-kitten relationship. Pages 23-39 *in* D. C. Turner and P. Bateson, eds. The domestic cat: the biology of its behaviour. Cambridge Univ. Press, Cambridge. 222pp.

Dyer, M. I. 1979. Conference summary: current status of North American bobcat programs. Pages 134-137 *in* P. C. Escherich and L. Blum, eds. Proc. 1979 bobcat research conference. Natl. Wildl. Fed. Sci. and Tech. Ser. 6.

Elder, W. H. 1952. Failure of placental scars to reveal breeding history in mink. J. Wildl. Manage. 16:110.

Englund J. 1970. Some aspects of reproduction and mortality in Swedish foxes (*Vulpes vulpes*) 1961-63 and 1966-69. Swedish Wildlife. 8:1-82.

Gashwiler, J. S., W. L. Robinette and O. W. Morris. 1961. Breeding habits of bobcats in Utah. J. of Mamm. 42:76-84.

Gilbert, F. F. 1987. Methods for assessing reproductive characteristics of furbearers. Pages 180-190 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Gosling, L. M. 1980. The duration of lactation in feral coypus (*Myocastor coypus*). J. Zool. Lond. 191:461-474.

Harris, S. 1979. Age-related fertility and productivity in Red foxes, *Vulpes vulpes*, in suburban London. J. Zool. Lond. 187:195-199.

Hersteinsson, P. 1984. The behavioural ecology of the arctic fox in Iceland. Ph. D. Thesis., Univ. of Oxford, Oxford.

Johnson, N. F. and D. J. Holloran. 1985. Reproductive activity of Kansas bobcats. J. Wildl. Manage. 49:42-46.

Knick, S. T., J. D. Brittell and S. J. Sweeney. 1985. Population characteristics of bobcats in Washington State. J. Wildl. Manage. 49:721-728.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildl. Monogr. 108, 1-42.

Lindstrom, E. 1981. Reliability of placental scar counts in Red fox (*Vulpes vulpes*) with special reference to the fading of the scars. Mamm. Rev. 11(4):137-149.

Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. Can. Wildl. Ser., Rep. Ser. 8. 52pp.

Martin, K. H., R. A. Stehn, M. E. Richmond. 1976. Reliability of placental scar counts in the Prairie vole. J. Wildl. Manage. 40(2):264-271.

Matson, G. M. 1981. Workbook for cementum analysis. Matson's Laboratories, Milltown, Montana. 30pp.

McCord, C. M. and J. E. Cardoza. 1982. Bobcat and lynx (*Felis rufus* and *F. lynx*). Pages 728-766 *in* J. A. Chapman and G. A. Feldhammer, eds. Wild mammals of North America: biology, management, and economics. John Hopkins Univ. Press, Baltimore, Md.

Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnisota. J. Mammal. 61:261-267.

Nava, J. A. 1970. The reproductive biology of Alaska lynx (*Lynx canadensis*). M. Sc. Thesis. Univ. of Alaska, Fairbanks. 141 pp.

Nellis, C. H., S. P. Whetmore, and L. B. Keith. 1972. Lynx-prey interactions in central Alberta. J. Wildl. Manage. 36:320-329.

O'Connor, R. M. 1984. Population trends, age structure, and reproductive characteristics of female lynx in Alaska, 1961 through 1973. M. Sc. Thesis. Univ. of Alaska, Fairbanks. 111 pp.

Payne, N. F. 1984. Reproductive rates of beaver in Newfoundland. J. Wildl. Manage. 48:912-917.

Poole, K. G. 1992. Lynx research in the Northwest Territories, 1991-92. Dept. of Ren. Res., Govt. of N. W. T. Manuscript report no. 68. 43pp.

Quinn, N. W. S., and J. E. Thompson. 1987. Dynamics of an exploited Canada lynx population in Ontario. J. Wildl. Manage. 51:297-305.

Quinn, N. W. S., and G. Parker. 1987. Lynx. Page 682-695 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer conservation and management in North America. Ontario Ministry of Natural Resources, Ontario.

Rolley, R. E. 1987. Bobcat. Pages 670-681 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer conservation and management in North America. Ontario Ministry of Natural Resources, Ontario.

Sanderson, G. C. and A. V. Nalbandov. 1973. The reproductive cycle of the racoon in Illinois. Ill. Nat Hist. Survey Bull. 31:29-85.

Sanderson, G. C. 1987. Racoon. Pages 486-499 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer conservation and management in North America. Ontario Ministry of Natural Resources, Ontario.

Saunders, J. K. 1961. The biology of the Newfoundland lynx, (*Felis canadensis subsolanus* Bangs). Ph. D Thesis, Cornell Univ., Ithaca, N. Y. 109pp.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles and J. P. Messick. 1973. Mountain lion social organization in the Idaho primitive area. Wildl. Monogr. no. 35.

Stewart, R. R. 1973. Age distributions, reproductive biology, and food habits of Canada lynx, (*Lynx canadensis* Kerr) in Ontario. M. Sc. Thesis, Univ. of Guelph, Ont. 61pp.

Van Zyll de Jong, C. G. 1961. The biology of the lynx, *Felis (lynx) canadensis* Kerr, in Alberta and the Mackenzie district, NWT. M. Sc. Thesis, Univ. of Alberta, Edmonton. 76pp.

GENERAL DISCUSSION AND CONCLUSIONS

Lynx (*Felis lynx*) recruitment changed dramatically with changes in hare (*Lepus americanus*) abundance during this study. Large litters and high survival demonstrated the massive potential for growth in Canada lynx. The adult cohort continued to reproduce for one year after hares declined but most yearlings discontinued reproduction the year of the decline. The abrupt cessation of reproduction by both adults and yearlings two years after the hare decline exemplifies the dependency of the lynx population on hares.

The mean adult litter size of over 5, and the fact yearlings can successfully breed demonstrates that North American lynx have a much greater capacity to increase than other similar sized felids. The bobcat (*F. rufus*), European wildcat (*F. silvestris*), Jungle cat (*F. chaus*), and Caracal (*F. caracal*) have similar size and life histories to the lynx though mean litter size is around 3 for all these species (Conde and Schauenberg 1974, Schauenberg 1979, McCord and Cardoza 1982:736, Bernard and Stuart 1987). Litter size in the smaller feral domestic cat populations (*F. silvestris*) varies, but there are reports of mean litter size close to those seen in this study (Jones and Coman 1982, Brothers et al. 1985, Deag et al 1988:31). The arctic fox (*Alopex lagopus*) is another northern predator whose main prey, lemmings (*Lemmus spp.*), cycle dramatically. And like the lynx, it too has larger litters than is characteristic of its family (Macpherson 1969, Garrott and Eberhardt 1987).

Lynx breed during hare low periods, even though they have little chance of rearing young. Litter size declines relatively little when hares decline (Brand and Keith 1979, O'Connor 1984). It appears that, as proposed by Brand and Keith (1979), the main mechanism limiting recruitment in cyclic lynx populations is the loss of young at or shortly after parturition. This strategy allows dispersing females the opportunity to reproduce if they locate an area with sufficient prey. Kitten survival was found to be the main factor affecting lifetime reproductive success in lions (*Panthera leo*), and it changed with food supply (Packer et al. 1988). In arctic foxes litter size changed little with large changes in prey abundance but pup survival changed markedly (Macpherson 1969).

Poor survival of kittens of yearling mothers has been reported for domestic cats (Deag et al. 1988) and for captive lynx (Alison Tokarchuk-pers. comm.). Deag et al. (1988) noted that primiparous females may be poorer mothers and that they lose more kittens than experienced mothers. They report that the parity of the mother had no effect on kitten weight during rearing. If experience is the cause of lower recruitment from yearlings then recruitment is not likely to be higher on trapped areas than untrapped areas. Heavily trapped areas would have very low recruitment due to their low average age; most recruitment is likely to come from immigration (Knick 1990).

Family group relationships in this population can be compared to other felids. Lynx kittens generally stayed with their mother for about 10 months. Kittens began to make solo movements in December and January but I did not see single kitten tracks regularly until the first of March. Occasionally I located female kittens with their mother until May when the mother gave birth again; and one kitten female gave birth to a litter within 800 m of its mother in 1990. Lynx kittens sometimes stay together after they have separated from their mother, though how long this persists is unknown. Saunders (1963), Brand et al. (1976), and Parker et al. (1983) found similar family group behaviour during their research on lynx in Newfoundland, Alberta, and Prince Edward Island. Lindemann (1955) found family groups of European lynx (*F. lynx*) remained together for 10 months while those of European wildcats separated after 5 months. Wassemer et al. (1988) found bobcat kittens stayed with the mother for an average of 9 months though some kittens remained with the mother until she had her next litter, as in lynx. Bailey (1979) found young bobcats stayed with mother up to one year and

he suggested males dispersed before females (Bailey 1981). Ross and Jalkotzy (1992) found sibling cougars (*F. concolor*) stayed together after independence and that female juveniles sometimes remained on their natal home range. Sunquist (1981) found that juvenile female tigers (*Panthera tigris*) established residences on their mother's home range. In summary, family group relationships in lynx are similar to other felids.

The bond between females and their female offspring appears to persist in lynx, as in lions (Bertram 1975) and perhaps cheetahs (*Acinonyx jubatus*) and other cats (Kleiman and Eisenberg 1973). Female offspring often remained on or near their mother's home range and I located mothers and their female offspring together regularly during this study even when both females had kittens. No similar relationship between mothers and their male kittens was observed. Kleiman and Eisenberg (1973) suggested the matrilineal bond is the main behaviour behind the social structure of lions. The matrilineal bond may affect social organization in lynx and other supposedly non-social felids.

Placental scar counts accurately predicted live litter size. They are probably slightly conservative when light (Shade 1) scars are excluded, but this will tend to over-estimate the effect of harvest, which is preferable. I believe placental scar counts are conservative because some scars never form properly or are faded by deterioration of the reproductive tract. The effect of carcass deterioration is easily investigated and warrants the effort. The accuracy with which pregnancy rate is predicted is less certain because the trapped sample may have had different pregnancy rates than the radio-collared population. Lembeck and Gould (1979) and Knick (1990) have shown that trapped and untrapped bobcat populations can have different reproduction rates. Pregnancy rates may not have been biologically different but trapping may have over-sampled some cohorts with respect to their abundance, which biased the pregnancy rate. The uncertainty with which a trapped sample predicts population parameters for the entire population continues to make the use of in utero counts questionable.

While placental scar counts give reasonable estimates of litter size and perhaps pregnancy rate when food is abundant, they cannot be safely used to estimate reproduction when food is limiting because of the likelihood of abortion or litter abandonment. Models that estimate the impact of harvest on feline populations such as those of Crowe (1975) and Knick (1990) for bobcats, and Brand and Keith (1979) for lynx need an estimate of kitten survival during periods of food shortage. Because kitten survival changes more with food supply than does the number of kittens born, measuring kitten survival may be more useful for monitoring population status or estimating reproduction than an estimate of litter size.

LITERATURE CITED

Bailey, T. N. 1979. Den ecology, population parameters and diet of eastern Idaho bobcats. Pages 62-69 *in* P. C. Escherich and L. Blum, eds. Proc. 1979 bobcat research conf. Natl. Wildl. Fed. Sci. and Tech. Ser. 6.

Bailey, T. N. 1981. Factors of bobcat social organization. Pages 984-1000 *in* J. A. Chapman and D. Pursley, eds. Proc. worldwide furbearer conf. Frostburg, Md.

Bernard, R. T. F. and C. T. Stuart. 1987. Reproduction of the caracal (*Felis caracal*) from the Cape Province of South Africa. S. Afr. J. Zool. 22(3):177-182.

Bertram, B. C. 1975. Social factors influencing reproduction in wild lions. J. Zool. Lond. 177:463-482.

Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40:416-428.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827-849.

Brothers, N. P., I. J. Skira, and G. R. Copson. 1985. Biology of the Feral Cat (*Felis catus* L.) on Macquarie Island. Aust. Wildl. Res. 12:425-436.

Conde, B., and P. Schauenberg. 1974. Reproduction du Chat forestier (*F. silvestris* Schr.) dans le nord-est de la France. Revue suisse Zool. 81(1):45-52. (in French with English summary).

Crowe, D. M. 1975. A model for exploited bobcat populations in Wyoming. J. Wildl. Manage. 39:408-415.

Deag, J. M., A. Manning, and C. E. Lawrence. 1988. Factors influencing the mother-kitten relationship. Pages 23-39 *in* D. C. Turner and P. Bateson, eds. The domestic cat: the biology of its behaviour. Cambridge Univ. Press, Cambridge. 222pp.

Garrott, R. A. and L. E. Eberhardt. 1987. Arctic fox. Pages 394-407 *in* M. Novak, J. A. Baker, M. E. Obbard, B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Jones, E., and B. J. Coman. 1982. Ecology of the Feral Cat (*Felis catus* L.), in south-eastern Australia II. Reproduction. Aust. Wildl. Res. 9:111-119.

Kleiman, D. G., and J. F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildl. Monogr. 108, 1-42.

Lembeck, M., and G. I. Gould Jr. 1979. Dynamics of harvested and unharvested bobcat populations in California. Pages 53-54 *in* P. C. Escherich and L. Blum, eds. Proc. 1979 bobcat research conf. Natl. Wildl. Fed. Sci. and Tech. Ser. 6.

Lindemann, W. 1955. The early development of lynx and the wildcat. Behaviour 8:1-45. (in German with English summary).

Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. Can. Wildl. Ser., Rep. Ser. 8. 52pp.

McCord, C. M., and J. E. Cardoza. 1982. Bobcat and lynx (*Felis rufus* and *F. lynx*). Pages 728-766 *in* J. A. Chapman and G. A. Feldhammer, eds. Wild mammals of North America: biology, management, and economics. John Hopkins Univ. Press, Baltimore, Md.

O'Connor, R. M. 1984. Population trends, age structure, and reproductive characteristics of female lynx in Alaska, 1961 through 1973. Msc. Thesis. Univ. of Alaska, Fairbanks. 111 pp.

Packer, C., L. Herbst, A. E. Pusey, J. D. Bygott, et al. 1988. Reproductive success of lions. Pages 363-383 *in* T. H. Clutton-Brock ed. Reproductive success:studies of individual variation in contrasting breeding systems. Univ. of Chicago Press, Chicago.

Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx on Cape Breton Island. Can. J. Zool. 61:770-786.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. J. Wildl. Manage. 56:417-426.

Saunders, J. K. 1963. Movements and activities of the lynx in Newfoundland. J. Wildl. Manage. 27:390-400.

Schauenberg, P. 1979. La reproduction du Chat des marias (*Felis chaus* Guldenstadt, 1776). Mammalia 43(2):215-223. (in French with English summary).

Sundquist, M. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal. Smithsonian Contributions to Zoology #336. Smithsonian Inst. Press. Washington, D. C. 98pp.

Wassmer, D. A., D. D. Guenther, and J. N. Layne. 1988. Ecology of the bobcat in south-central Florida. Bull. Florida State Mus. Biol. Sci. 33(4):159-228.